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Shifting Patterns of Ribbed Mussel Distribution and Ecosystem Services in Response to Sea Level Rise

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Shifting patterns of ribbed mussel distribution and ecosystem services in response to sea level rise

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This Ph.D. is dedicated to my wife, Mary Isdell, who has been an unwavering supporter and advocate as I have pursued my passion.

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ABSTRACT

Throughout the salt marshes of the US Atlantic Coast, ribbed mussels (*Geukensia demissa,* Dillwyn, 1817) and smooth cordgrass (*Spartina alterniflora* Loisel) form an important mutualistic relationship. *Spartina* provides habitat and promotes settling of ribbed mussels, which, in turn, stabilize and fertilize the *Spartina* and sediment. This relationship, however, is at risk of interruption due to sea level rise, erosion, and coastal development. Among the most at-risk segments of the marsh, the front (waterward) edge of the marsh is also where ribbed mussels and their ecosystem services are concentrated. Despite their importance of ribbed mussels to the salt marsh ecosystem, very little is known about the spatial distribution. In order to address these questions, we had the following objectives: 1) to identify spatial factors influencing mussel distribution across the landscape, 2) to quantify the contribution of ribbed mussels to nitrogen removal in the presence of *Spartina*, and 3) to assess how the distribution of the population and its ecosystem services are likely to change by the year 2050.

We conducted field work in the summers of 2015 and 2016 to survey ribbed mussel populations in 30 marshes around the Chesapeake Bay. Ribbed mussel population density and distribution was positively related to the number of *Spartina* stems, the exposure of the site, and to a minor degree, the amount of agriculture within 300 m. The amount of forested land cover within 60 m was negatively related to ribbed mussel density. With these factors, we built a model to estimate ribbed mussel populations in the first two meters (edge) of the marsh, and estimated the presence of 805 million mussels along the edges of Virginia's marshes. Sediment core incubations revealed that when ribbed mussels are integrated with *Spartina*, the ammonium and particulate removal is enhanced, relative to when mussels occur separately, but that the overall rates vary dramatically by the location of the marsh whence the cores were collected. Spatial application of a 0.62 m sea level rise scenario and local erosion rates altered the distribution of both marshes and ribbed mussels. Overall, ribbed mussel abundance declined by 3.6% between 2018 and 2050; however, most locations saw moderate to large declines, while a very few locations saw very large increases (> 100%). Declines in abundance were greatest in urban areas dominated by fringing marsh and extensive shoreline armoring, while gains were greatest in agricultural areas with extensive marshes. The projected redistribution of mussels by 2050 will have important implications for water quality improvement goals that will need to be addressed by local and state authorities.

This dissertation has focused on the seascape ecology and management of ribbed mussels in the Chesapeake Bay. The work has demonstrated the importance of applying spatial techniques to study and understand organisms and ecosystems at the interface between land and water. Only through further study and proactive planning will we be able to plan for and address the coming impacts of anthropogenic climate change and sea level rise.

Shifting patterns of ribbed mussel distribution and ecosystem services in response to sea level rise

CHAPTER 1

Introduction

INTRODUCTION

The intertidal zone is one of the most challenging environments on Earth for sessile plants and animals (Chelazzi and Vannini 2013). Subject to frequently alternating inundation and exposure, the organisms that live in the intertidal must be able to cope with an extremely wide range of physical conditions. Despite the immense challenges to life in the intertidal, it is home to one of the most productive ecosystems on the planet, the salt marsh (Lieth 1972). Throughout the temperate zones of the world, salt marshes dominate the intertidal (Mitsch and Gosselink 2015), providing a wealth of ecosystem services (Zedler and Kercher 2005, Cooper 2005). From water quality improvements (Gedan et al. 2009) to blue carbon storage (Mcleod et al. 2011) to habitat provisioning, salt marshes are invaluable to the coastal environment (Barbier et al. 2010).

Along the US Atlantic Coast, salt marshes are home to the ribbed mussel, *Geukensia demissa*. The ribbed mussel is a bivalve filter feeder in the family Mytilidae, and occurs from Cape Cod, MA to southern Florida where it is replaced in the Gulf of Mexico by its congener *Geukensia granosissima* (Honig et al. 2014, Harasewych and Moretzsohn 2014). The ribbed mussel has a modioliform body-type, as indicated by its rounded anterior, which is typical of mussels that live in soft sediments (Sarver et al. 1992). Ribbed mussels have planktonic larvae which remain in the water column for 12-16 days (Justin Manley, pers. comm.) before metamorphosing. At the competent-to-settle stage, ribbed mussel larvae are small enough (Baker and Mann 2003) to still be influenced by the high viscosity fluid dynamics that dictate the movement of particles and organisms with low Reynold's numbers (Vogel 1994).

Ribbed mussels bury into the marsh where they use their byssal threads to attach to the roots, rhizomes, and stems of *Spartina* (Bertness 1984). Once attached, these mussels form a mutualistic relationship with *Spartina*. The byssal threads stabilize the sediment, thereby reducing erosion and improving the stability of the marsh. Ribbed mussels also fertilize the marsh through their biodeposits of feces and pseudofeces and ammonium excretion (Jordan and Valiela 1982). This stabilization and fertilization combine to increase the growth and density of the *Spartina*, which in turn, attracts more mussels. More stems induce more settlement, and so more mussels are likely to settle in denser patches of *Spartina* than in sparse patches (Angelini et al. 2016). In this way, mussels and *Spartina* form a positive feedback loop.

Ribbed mussels play an important role in the marsh nitrogen (N) cycle. As filter feeders, they filter out particles, and ingest ~50% of the N that they filter, while the rest is deposited in pseudofeces on the marsh surface (Jordan and Valiela 1982). Of what they ingest, ~50% of the N is excreted as ammonium, and the remaining 50% is stored in somatic and germ tissues (Jordan and Valiela 1982). Beyond their conversion of particulate N to tissue and mineralized N, ribbed mussels also contribute to N removal via denitrification (DNF). When paired with *Spartina*, ribbed mussels enhance DNF to levels greater than either could achieve separately (Bilkovic et al. 2017). This enhanced N removal, along with ribbed mussels' ability to very efficiently remove a wide range of particulates from the water column (Kreeger and Newell 2001), make them important contributors to local water quality (Isdell, Chapter 4, this dissertation).

Unfortunately, both marshes and their inhabitants are being displaced by climate change and the resulting sea level rise (SLR) (Mitchell et al. 2017, Shepers Lennert et al.

2017). Typically, in times of slow to moderate sea level rise, marshes maintain their vertical position within the tidal envelope by accreting sediment and organic matter at a rate roughly equal to SLR (Vernberg 1993). A marsh's horizontal position (i.e., spatial location and aerial extent) in relation to the shoreline is dependent on rates of erosion at the front (waterward) edge of the marsh, and landward migration at the back edge of the marsh; however, as SLR is accelerating in many places around the world, the balance between accretion and landward migration is at risk. In the Chesapeake Bay, Virginia, USA, the long-term stability of the marshes is increasingly unlikely (Mitchell et al. 2017). The Chesapeake Bay is a microtidal system with relatively low suspended sediment concentrations, extensive coastal development, and has the second fastest rate of relative SLR (RSLR – the combined rates of global sea level rise as well as other local factors such as land subsidence; 5.14 mm/yr) in the US (Boon and Mitchell 2015). In the Chesapeake Bay, RSLR has already exceeded the maximum expected rate (5 mm/yr) of marshes accretion (Kirwan et al. 2010). Further, approximately 18% of the shoreline in the Bay has been armored to prevent erosion (Bilkovic et al. 2016). This armoring serves to both reduce the sediment supply and prevent the inland migration of the marshes (Torio and Chmura 2013), resulting in coastal squeeze (Pontee 2013). Coastal squeeze occurs when the front edge of the marsh is eroding faster than the back edge can migrate inland, resulting in a narrowing, and eventual disappearance of the marsh.

The combination of the importance of ribbed mussels to the marsh ecosystem, and the threats facing salt marshes are the impetus for this dissertation. Contained within are three works related to the spatial distribution of ribbed mussels and their ecosystem services. Chapter two focuses on identifying spatial factors that drive variations in mussel

populations around the Chesapeake Bay. From these factors, a mussel distribution model (MDM) was developed to generate spatially explicit predictions of mussel density along the front edge of marshes. Chapter three focuses on quantifying the N removal potential of ribbed mussels from different marshes. Finally, Chapter four focuses on applying the MDM to a future SLR scenario, and comparing the population ecosystem service distribution between the present and 2050.

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CHAPTER 2

Shorescape-level factors drive distribution and condition of a salt marsh facilitator (*Geukensia demissa* Dillwyn, 1817)

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ABSTRACT

Ribbed mussels (*Geukensia demissa*) are a highly abundant bivalve filter feeder throughout the salt marshes of the United States Atlantic coast. These mussels form a mutualistic relationship with smooth cordgrass *Spartina alterniflora* wherein the grass provides habitat and shade to the mussels, and the mussels stabilize the sediment and fertilize the grass. Salt marshes are, however, rapidly changing and eroding as humans modify the coast and the rate of sea level rise is accelerating. In order to understand how ribbed mussels may respond to their changing habitat, we collected mussel density and distribution data from 30 marshes covering the range of geomorphic settings found in lower Chesapeake Bay. We used a combination of *in-situ* and GIS derived spatial variables to develop spatially applied models of ribbed mussel density and physical condition. Of the estimated 1.06 billion ribbed mussels in Virginia, we found that mussels were most abundant along the front edge of marshes in wide creeks, rivers, or bays with dense *Spartina* and minimal proximal forest, set in agriculturally dominated areas. In contrast, mussel condition was highest in fringing marshes located in narrow tidal creeks. Ribbed mussels responded to factors at a variety of scales, ranging from extremely local (0.25 m) to larger shorescapes (≥ 300 m). The methods that we used to create models linking both aquatic and terrestrial variables to explain the variation in ribbed mussel populations along the shoreline provide a valuable tool for identifying baselines and assessing potential for change across estuary-level spatial scales not only for ribbed mussels in the Chesapeake Bay, but also for other sessile, intertidal species in other systems.

INTRODUCTION

Salt marshes are one of the major vegetated interfaces between land and water throughout the world's temperate zones, and are among the most productive ecosystems on the planet (Lieth 1972), providing a wealth of ecosystem functions and services including wave energy reduction and erosion control (Cooper 2005), nitrogen removal (Valiela and Teal 1979, Nelson and Zavaleta 2012), and habitat provisioning (Díaz-Ferguson et al. 2010, Valiela 2015, Angelini et al. 2015). Unfortunately, marshes have been shrinking due to a number of natural and anthropogenic causes such as sea level rise (Craft et al. 2008, Bilkovic et al. 2009), coastal development such as housing and roads (Kittinger and Ayers 2010, Bilkovic et al. 2016), and natural and boat wake induced erosion (Schwimmer 2001, Silinski et al. 2015). On the East Coast of the United States, smooth cordgrass (*Spartina alterniflora* Loisel.; simply *Spartina* hereafter) dominates the lower marsh (more frequently inundated), while salt meadow hay (*Spartina patens* (Ait.) Muhl.) dominates the upper marsh.

Integrated into the surface of the salt marsh are ribbed mussels (*Geukensia demissa* Dillwyn, 1817). Ranging from Cape Cod, Massachusetts to southern Florida, ribbed mussels form a mutualistic relationship with *Spartina* in the low marsh (Bertness 1984). The ribbed mussel lives in the brackish intertidal zone in salinities from 8-30‰ (Lent 1969). Ribbed mussels typically burrow down into the sediment where they bind their byssal threads to the roots, rhizomes, and stems of *Spartina* (Lin 1990), while leaving their posterior end exposed above the surface. By attaching themselves to these plant structures, they also bind the sediment, thereby increasing the stability of the marsh by reducing erosion (Moody 2012). Ribbed mussels are also noted for being extremely

efficient filter feeders (Galimany et al. 2015). Their ability to improve water quality rivals that of oysters, and even exceeds oysters at the smallest particle sizes (Kreeger and Newell 2001). While filter feeding, ribbed mussels excrete ammonia, which effectively serves to fertilize the smooth cordgrass (Jordan and Valiela 1982). The fertilized *Spartina* increases its aboveground biomass, which then facilitates increased sedimentation (Bertness 1984). This partnership between ribbed mussels and *Spartina* results in a more resilient marsh (Smith and Frey 1985).

Ribbed mussels are bivalves in the family Mytilidae (Ruppert et al. 2003) that exhibit external fertilization with planktonic veliger larvae. The larvae remain in the water column for 12-45 days, where they grow to ~200 µm. During the pediveliger stage (~ 200+ µm), they maintain a position in the upper water column, likely to maximize their chances of moving onto the marsh with an incoming tide (Baker and Mann 2003). Larvae are most likely to initially settle on structure, such as *Spartina* stems, and then metamorphose (Porri et al. 2007). After metamorphosis, juveniles may further disperse either short or long distances to select for better habitat (Franz 2001). Post-settlement movement is thought to cease once the mussels reach sexual maturity—around 25 mm (Franz 2001).

Ribbed mussels are not distributed homogeneously across the surface of the marsh. In general, ribbed mussel densities are typically highest at the front (seaward) edge of the marsh, and decline with increasing distance into the marsh (Bertness and Grosholz 1985, Bilkovic et al. 2017). Throughout their range, ribbed mussels self-organize into dense aggregations, ranging from 0 – 7,000 individuals m^{-2} (Bertness and Grosholz 1985, Stiven and Gardner 1992). The causes of the variation in mussel densities

are unclear at large scales, given that very few studies have examined ribbed mussel distribution across multiple marshes (Angelini et al. 2016, Bilkovic et al. 2017), and to our knowledge no studies have attempted to identify the spatial scales at which land- and seascape factors are important. At small scales, researchers have identified a clear, positive relationship between ribbed mussel densities and smooth cordgrass stem densities (Bertness 1984, Angelini et al. 2015) as well as a possible preference for adult conspecifics. This is unsurprising given the mutualistic relationship between the two species, though the causality (ribbed mussels increasing stem densities, or increased stem densities attracting more ribbed mussels) is still debated (Hughes et al. 2014).

The role of ribbed mussels as a salt marsh facilitator has been explored for the past couple of decades in a variety of regions along the US Atlantic Coast (Bertness and Leonard 1997, Angelini et al. 2015, 2016). Ribbed mussels improve the marsh not only for the *Spartina*, but for the other organisms found there as well. The tendency of ribbed musseels to aggregate into large groups results in increased moisture retention and the creation of microclimates. Moisture retention by aggregates of adult ribbed mussels provides a more stable environment for the juvenile ribbed mussels as well as other benthic invertebrates. The stabilized marsh resulting from the *Spartina*/ribbed mussel mutualism also supports increased species richness and functional diversity (Angelini et al. 2015). Increased ribbed mussel abundances further attracts predators such as blue crabs (*Callinectes sapidus*), Atlantic mud crabs (*Panopeus herbstii*), black ducks (*Anas rubripes*), and raccoons (*Procyon lotor*), which all feed extensively on ribbed mussels (Seed 1980, Brousseau 1984, Bertness and Grosholz 1985, Lin 1990, Eichholz et al. 2009). In addition to facilitating diversity and resilience, ribbed mussels are also

important for their role in nitrogen removal. Recent studies (Bilkovic et al. 2017) have suggested that the mutualism between *Spartina* and ribbed mussels may increase the rate of denitrification in marshes (Bilkovic et al. 2017), thereby providing a valuable ecosystem service that contributes to water quality management goals throughout their range. Taken all together, the ecosystem functions provided by ribbed mussels make them a vital member of the marsh community along the US Atlantic Coast.

Relatively little is known about how ribbed mussels are likely to respond to the previously noted rapidly changing environmental conditions, and even less is known about their responses in estuaries with lower (<25 ppt) salinities. It is important to document broad distributions of ribbed mussels and evaluate factors that may limit the capacity of ribbed mussels to facilitate diversity, stabilize marshes, and enhance water quality at both a regional scale (shorescape, defined here as the zone along tidal shorelines encompassing riparian, intertidal, and near-shore littoral areas) and a local scale (within the marsh). This study was performed with the following objectives: 1) to determine the primary local and shorescape factors influencing the current distribution and condition of ribbed mussels within a marsh and throughout an estuary and 2) to use empirically derived relationships to model ribbed mussel distribution throughout the lower Chesapeake Bay, Virginia.

METHODS

Study Area

Our study area encompassed the lower Chesapeake Bay (Figure 1), Virginia, USA. Salinities in our study area ranged from 8-22 ‰ while water temperatures vary annually from ~3 – 32 ℃. Marshes selected for the study were exclusively *S. alterniflora*

dominated in the low marsh, while the high marsh was typically *S. patens* dominated, with occasionally high densities of *Distichlis spicata* (L.) Greene. *Juncus romerianus* (Scheele) was often found in the transition zone from low to high marsh.

Site Selection

Study sites were selected from the Eastern Shore of Virginia, the York River, and Mobjack Bay using a stratified random sampling approach to target marshes in a variety of settings within 5 km of water or terrestrial access locations. Access locations included public and private boat launches, roads, and homes. In total, 30 sites (Figure 1) were randomly selected using ArcGIS 10.0 (ESRI 2011) and Geospatial Modeling Environment (Beyer 2012) along an exposure (i.e., open water area within a 500-m radius) gradient. Sites were accessed by kayak, canoe, or motor boat.

Field Sampling

We sampled each site once during the summer months (June – August) of 2015 (N=13) and 2016 (N=17). At each site, we sampled 4 transects, spaced at least 5 m apart, inward from the water toward the upland. Transects were sampled using a 0.25 m^2 quadrat, placed to span the first 50 cm of each meter, every meter for the first 5 m of marsh. We counted the number of juvenile (<20 mm shell length) and adult ribbed mussels in each quadrat for each transect. In addition to the ribbed mussels, we recorded plant species, height, and shoot density for each quadrat. We also recorded the distance from water to the last ribbed mussel along the transect if the distance is >10 m. Up to 20 adult and juvenile ribbed mussels representative of the size distribution on site were collected at each distance from the edge to be processed in the laboratory for condition indices (see below). Ribbed mussels were not collected if absent or in extremely low

abundance for a given distance within a marsh. Each collected ribbed mussel was measured (height, length, width), weighed for total wet weight (shell and tissue combined (g)), then shucked into pre-weighed aluminum weigh boats (shell and tissue separately), dried at 65 ℃ for 48 h, and reweighed.

In addition to counts of flora and fauna, we recorded physical characteristics of each site. Marshes were categorized as platform or non-platform marshes based on the morphology of the front edge of the marsh. If the front edge of the marsh was actively eroding with a steep, often vertical face from the *S. alterniflora* to the subtidal, the marsh was classified as a platform marsh. All other marshes were classified as non-platform marshes. We also recorded the salinity (ppt) at each site using a salinity refractometer, as well as water temperature (℃) using a digital thermometer.

Condition Index

Condition indices have been used to describe an individual bivalve based on the amount of mass it has allotted to its shell vs. soft tissue, adjusted for its volume (Crosby and Gale 1990). Ribbed mussels with a high condition index would have a higher soft tissue weight to shell ratio than mussels with a low condition index. If the relative amount of soft tissue weight is low, then environmental conditions are likely unfavorable. A condition index for each mussel was calculated using Equation 1 (Crosby & Gale, 1990):

Eq 1. $$CI = \left(\frac{dry\ soft\ tissue\ wt\ (g) x\ 1000}{internal\ shell\ cavity\ capacity\ (g)}\right)$$

where internal shell cavity capacity is calculated as the total wet weight of the individual – the dry shell weight. Although the term internal shell cavity capacity gives the

impression of volume, it actually represents the ratio of dry tissue to wet. A shell-to-tissue ratio (STR) was also calculated using Equation 2.

Eq 2. $$STR = \frac{dry\ shell\ wt\ (g)}{dry\ tissue\ wt\ (g)}$$

Geospatial Variables

Shorescape variables were obtained using ArcGIS v.10.4.1 (ESRI 2011). Given known impacts of surrounding land use on a variety of marine and aquatic organisms (Seitz et al. 2006, Bilkovic and Roggero 2008, Isdell et al. 2015), we identified the proportion of agriculture, forest, marsh, and impervious surface within increasing concentric circles (neighborhoods) of the site. Land use data was derived from the VA CCAP land cover dataset (1-m pixel resolution; resampled to 5-m pixel resolution using a majority assignment). We selected radii from 20 m – 2000 m (20, 40, 60, 80, 100, 150, 200, 300, 400, 500, 1000, 1500, and 2000 m) to span the range of local to watershed level impacts. We also included the percentage of water within the same radii of a site to serve as a proxy for exposure (defined as the amount of physical energy from waves and tidal flow to which a location is subjected). Sites along a straight shoreline with a wide channel (e.g., a river) would have ~50% water at greater distances, while sites in narrow tidal creeks would have a much lower % water. We included this descriptor given that a previous study in the area (Bilkovic et al. 2017) found increased densities of ribbed mussels along large waterbodies and other highly exposed shorelines when compared with marshes in less exposed settings.

Statistical Analyses and Spatial Application

All statistical analyses were conducted using R (R Development Core Team 2011). To model ribbed mussel density, we used the site averaged quadrat density (adults and juveniles; Σ(mussel abundance in quadrats of first two meters of all transects at a site / number of quadrats), with a log(X+1) transformation to meet assumptions of normality. Using the site average eliminates any potential for pseudoreplication. Average ribbed mussel condition index (calculated the same as mussel density) for the first two meters of a site was the response variable for condition index models. We used a generalized linear model (function glm() in base R) with a Gaussian distribution for all analyses given the lack of fixed effects. We used a two-tiered approach to variable selection and model selection. We selected stem density, % water, % marsh, % forest, % agriculture, and % impervious surface as predictor variables, and evaluated all spatial variables at the 13 radii from 20 m – 2000 m. All variables were first run in univariate models to identify those with a lower AICc value than the null model ($y_i = \beta_0$). For each spatial variable, if multiple scales were better than the null model, the scale with the lowest AICc value was selected. Only variables with AICc values lower than the null model were selected for multiple linear regression (Table 1). All selected variables were checked for autocorrelation using the Pearson correlation coefficient (PCC; function cov() in base R) prior to their inclusion in any model. If autocorrelation was found (PCC ≥ 0.7; (Leu et al. 2011)), only one of the autocorrelated variables was included. All possible combinations of the variables were then allowed to compete (Doherty et al. 2012). The top models with a cumulative ≥ 95% of the AICc weight were then model averaged (Burnham and Anderson 2002), resulting in a final model. The final model predictions were compared

to the original data to obtain an R^2 value. The model was then spatially applied to the study area using the "raster calculator" tool in ArcGIS 10.4.1 to obtain ribbed mussel density estimates along the marsh edges by holding any on-site, non-spatially derived variables at their mean value. The total estimated number of ribbed mussels in Virginia was obtained by extracting only the raster cells along the front edge of the marshes. We converted that to a total number of mussels per cell by multiplying the value times 10 (length of cell [5 m] X first two meters) because each cell represented the number of ribbed mussels per m^2. The resulting values were summed to get the total. We also ran two additional scenarios in which we examined a low estimate (1^{st} quartile value of the variable) and a high estimate (3^{rd} quartile value of the variable) because the local variables had to be held constant. Total mussel estimates for the two additional scenarios were calculated the same way as described above.

We used an independently collected dataset (Bilkovic et al. 2017) of ribbed mussel density at the front edge of the marsh (N=20) for model verification. Spatial variables for each site were extracted to each point using ArcGIS v. 10.4.1. The model averaged formula was then applied to each site to obtain predicted values. Predicted values were compared to observed values to obtain an R^2 value to assess goodness of fit.

RESULTS

Mussel Distribution

Throughout the study area, ribbed mussel densities ranged from 0 – 3,808 mussels$\cdot m^{-2}$. Overall, ribbed mussel densities declined from the edge to the interior of the marsh (Figure 2), with the vast majority of the ribbed mussels (84.2%) being located within the first two meters of the marsh. Both adult and juvenile ribbed mussel densities

displayed nearly identical patterns of decreasing density with increasing distance into the marsh. Exposure at the marshes ranged from 6.7% water to 78.4% water within a 500-m radius. Exactly half of the observed marshes (N=15) were classified as platform marshes on site. Mean exposure at the front edge of the marsh (± S.E.) was 50.8 ± 5.1 % for platform marshes, and 30.0 ± 4.8 % for non-platform marshes. Ribbed mussel density was considerably higher on platform marshes (374.0 ± 94.8) than on non-platform marshes (58.5 ± 17.0; Figure 3). Water temperatures at the study sites ranged from 22.2 – 35.6 ℃ in the water immediately adjacent to the marsh at the time of sampling.

Ribbed mussel density was nearly homogeneous in marshes beyond the first two meters, making statistical inferences about among site variations difficult. As such, we focused our statistical efforts on the front edge (first two meters) of the marsh, where the majority of the population and greatest variation among sites was observed. The univariate modeling indicated that *Spartina* stem density (on-site count), % water (300-m radius), % forest (60-m radius), and % agriculture (300-m radius) all performed better than the null model based on AICc values (Table 1; Figure 4). Note that the distance for % water identified as the best explanation of ribbed mussel density via AICc (300 m) differs from the scale we originally selected for our exposure gradient (500 m). The Pearson correlation coefficient matrix indicated that there was not significant autocorrelation (all R^2 values less than 0.25), and could be included together in subsequent models. All possible combinations of the variables were then run (16 models), and the top 7 (cumulative AICc weight = 0.95) were selected for model averaging (Table 2). The final, averaged model was:

$$\log(mussels) = 0.5337 + 0.0363 * Stems + 0.0125 * \%\, Water - 0.0133 * \%\, Forest + 0.0009 * \%\, Agriculture$$

and had an adjusted R^2 value of 0.48.

Using the independent dataset for model verification, the predicted vs. observed had a significant, positive slope ($p < 0.001$) and an R^2 value of 0.62. After spatial application of the model (Figure 5), we estimate that there are 1.06 billion ribbed mussels along the front edges of Virginia's Chesapeake Bay marshes. Varying the stem density from the 1st quartile (120.24 stems·m^{-2}) to the 3rd quartile (254.76 stems·m^{-2}) provided estimates of 0.43-1.47 billion ribbed mussels.

Condition Index

Overall, condition index significantly ($p = 0.002$) declined with increasing distance into the marsh (Figure 6). Again focusing on the front edge (0 to 2 m into the marsh) site-averaged data (N = 24), only ribbed mussel density and % marsh within a 500-m radius (Figure 4) were found to have lower AICc values than the null model. With only two variables, we used a linear model to assess how well they explained the data. Using scaled and centered variables to better estimate the effect size of each variable, the resulting model was:

$$Condition\ Index = 88.51 - 10.17 * \log(mussels) - 6.15 * \%\, marsh$$

and had an adjusted R^2 value of 0.46. Thus, effect sizes were similar for both mussel density and % marsh, with mussel density having a slightly larger effect.

When considering the complete dataset (N = 1,381), condition index significantly ($p < 0.001$) decreased with increasing shell length when accounting for variations due to

site and distance into marsh. While the overall trend may have been negative, trends within a given site were much more variable with no clear pattern. Within a given marsh, ribbed mussel condition index may increase, decrease, or remain static with increasing shell length (see Figure 7 for typical responses). Shell-tissue ratios for the ribbed mussels showed no clear pattern with increasing distance into the marsh (Figure 8). However, the log-transformed STR showed a clear and significant ($p < 0.001$) increase with increasing % water within 500 m (Figure 9). The STR showed no association with ribbed mussel length ($p = 0.825$).

DISCUSSION

Distribution and Condition Index

We found that ribbed mussels were most abundant along the front edge of marshes in wide creeks, rivers, or bays with dense *S. alterniflora* and minimal proximal forest, set in agriculturally dominated areas. In contrast, ribbed mussel condition is likely to be highest in fringing marshes located in narrow tidal creeks. This is the first known instance in which the impacts of shorescape-level factors on ribbed mussels have been synthesized into a framework that allows for broad spatial application.

The decrease in ribbed mussel density with increasing distance into the marsh provides additional support for the long-standing, recognized ecological importance of the front edge of the marsh (Bertness 1984, Peterson and Turner 1994). Numerous species, ranging from decapods and molluscs to fish and reptiles, use and rely on the front edges of marshes as critical habitat where they obtain food and shelter (Peterson and Turner 1994, Silliman and Bertness 2002, Whitelaw and Zajac 2002). Angelini et al. (2015) suggested that ribbed mussels are important or even responsible for increased

diversity within the marsh. The decreasing ribbed mussel density with increasing distance into the marsh is likely a result of a combination of factors including particle settling dynamics, conspecific attraction, and inundation duration. Competent-to-settle pediveliger ribbed mussels are still small enough (Baker and Mann 2003) to be influenced by the high viscosity dynamics which apply to organisms and particles with low Reynold's numbers (Vogel 1994). At low Reynold's numbers, drag on particles is sufficiently great that particle movement is almost entirely controlled by the surrounding fluid. As such, ribbed mussel larvae are likely to settle out of suspension when they encounter the *S. alterniflora* at the front edge of a marsh which baffles the water and reduces flow, with fewer and fewer larvae remaining in suspension with increasing distance into the marsh (Leonard and Luther 1995, Christiansen et al. 2000, Leonard and Croft 2006). Ribbed mussel larvae are attracted to adult conspecifics, potentially resulting in a positive feedback loop at the front edge of the marsh (Nielsen and Franz 1995). The front edge of the marsh is inundated for longer than any other part of the marsh over a tidal cycle, resulting in increased feeding opportunity and decreased thermal and desiccation stress (Chapman and Underwood 1996, Charles and Newell 1997), which are essential for the highly vulnerable, recently metamorphosed juveniles. Our observations of ribbed mussel distribution patterns in brackish systems are consistent with previous observations from euhaline systems (Bertness and Grosholz 1985, Stiven and Gardner 1992). The above explanations for why ribbed mussels are most abundant at the edge are similarly applicable as reasons for why *Spartina* stem density was the most important predictor in the mussel density model. The effects of *Spartina* on settling and survival likely increase with increasing stem density along the edges of marshes. Marshes with

lower *Spartina* stem density are less likely to baffle the water and promote settlement, and after settlement, will provide less shading and predator protection. All else being equal, the increased stresses of a low *Spartina* stem density marsh edge should result in decreased ribbed mussel density relative to higher *Spartina* stem density marsh edges.

Ribbed mussels may be more abundant in wider, more exposed waterbodies for a variety of reasons. The percentage of water within a 300-m radius of a site is likely a proxy for exposure, rather than a direct driver. Three-hundred meters may also be the scale at which scarping begins to occur, thereby resulting in the platform marshes which supported much higher densities of ribbed mussels. Alternatively, delivery of particulate matter (Temmerman et al. 2005a, 2005b), such as food and larvae, and tidal flushing of sediments (Wilson and Gardner 2006) may all be greater in more expansive waters. The preceding possibilities are further supported by the shell-to-tissue ratio (STR) results. The increased STR at higher %-water values (Figure 9) indicates that ribbed mussels in more exposed sites are either putting more resources into shell growth, or less into soft tissue. It is possible that increased shell thickness in more exposed sites may be a result of increased wave exposure or predation pressure in those areas. Alternatively, density-dependent competition may be occurring in the higher exposure sites where mussels are more concentrated, resulting in fewer resources for soft-tissue (Franz 1993). One additional possibility is that ribbed mussels in the higher exposure sites simply put more effort into reproduction (i.e., a greater proportion of soft tissue is dedicated to gamete production than somatic growth). Indeed, Franz (1993, 1997) has shown that ribbed mussels provided with an abundance of food will increase gametic output compared to those provided with fewer resources. Furthermore, Borrero (1987) has noted that even

within a site, variable access to resources driven by reduced feeding times as a function of increasing distance into the marsh can result in delayed gamete production. This delay in reproduction may span several months, making within-site reproductive timing potentially more variable than latitudinal, temperature driven reproduction. All of these possibilities may contribute to the highly variable length-condition index relationships shown in Figure 7.

Coincident with increased exposure is increased erosion. The marshes where ribbed mussels are most abundant are also where erosion rates are likely to be highest. While ribbed mussels may be able to respond to a limited amount of erosion by colonizing the marsh immediately behind the edge, there is likely a limit to this capability. Researchers in Delaware Bay, US, have noted that while ribbed mussel presence is correlated with reduced erosion, it is only in the less exposed reaches of their habitat (Moody 2012). In order for there to be high densities of ribbed mussels that include adults (>25 mm, ~1-2 years old) along the front edge of the marsh, erosion rates should not exceed 1 $m \cdot yr^{-1}$ to allow for the growth rate of ribbed mussels and their recruitment patterns to keep up with erosion. Greater erosion rates would require high densities of ribbed mussels beyond the front edge of the marsh to already be established before erosion reached the previously interior location in the marsh, which is unlikely given the precipitous decline in ribbed mussel density with increasing distance into the marsh observed in this study.

Agriculture was an important predictor of ribbed mussel density at a scale of 300 m. Mussels are likely responding to localized effects of agriculture, rather than whole watershed (Figure 4). Other examples of agricultural impact on the nearshore

environment are numerous, and have ranged from runoff carrying nutrients, sediment, and chemicals (Jordan et al. 2003, Vymazal and Březinová 2015), to increasing movement of synanthropic predators across the landscape (Beasley and Rhodes 2010). All of these may have an impact on ribbed mussels. Elevated nutrients help to fuel phytoplankton and benthic microalgae, important food sources for ribbed mussels at both juvenile and adult stages (Kreeger and Newell 2001, Jacobs et al. 2015). Increased nutrients also enhance aboveground growth of *S. alterniflora* (Darby and Turner 2008, Deegan et al. 2012), thereby increasing both stem density and shading potential. Increased sediment input may also help the marsh to maintain its height profile as the sea level rises (Morris et al. 2002). Thus, marshes in close proximity to agriculture may be more stable, allowing for better long-term establishment of mussel populations. Other studies have found that sediment input from agriculture has contributed to marsh areal growth (Baldwin et al. 2012). Contrary to the possible mechanisms for agriculture benefiting mussels, agriculture may also negatively impact mussels through the use of chemicals such as insecticides. Some insecticides have been observed to inhibit byssal thread formation (Ayad et al. 2011) while others inhibit the activity of acetylcholinesterase, an enzyme responsible for muscle relaxation (Fulton and Key 2001). Besides chemicals, agriculture is also known to attract a variety of synanthropic predators (Leu et al. 2008), such as raccoons, which are known to feed on ribbed mussels (Stiven and Gardner 1992). The small effect of agriculture compared to the rest of the variables in the model may be a result of all of these effects offsetting each other. Despite the scale being 5X larger than forested land use, it is still relatively localized—only encompassing the nearest field or two. A scale of 300 m, therefore, may indicate that

variation in the farming practices of individual farmers, such as riparian buffer width and fertilizer use, could be more important than how much farming is occurring within the watershed.

The negative relationship between ribbed mussels and nearby forest is more than likely an indirect effect or association than a direct impact. The relatively small scale of forest's influence at 60 m could be indicative of the effects of shading on *Spartina* growth and density (Chen et al. 2005). In very narrow fringing marshes, riparian overhang may be sufficient to detrimentally shade the *Spartina* underneath, thereby resulting in reduced growth and stem density. Alternatively, the negative relationship between ribbed mussels and nearby forest could also be an indicator of marshes suffering from coastal squeeze (Pontee 2013). If erosion rates outpace landward migration of the marsh, the marsh will eventually disappear. Coastal squeeze has been noted in a number other systems (Doody and Williams 2004, Torio and Chmura 2013), and represents one of the major ecological concerns for intertidal habitats with accelerating SLR. In one of the major sub-estuaries of the Chesapeake Bay, the York River, researchers identified that fringing and extensive marshes were the most at-risk marsh types, while embayed marshes are doing well (Mitchell et al. 2017). The areas of greatest loss were developed watersheds with greater exposure dominated by fringing marshes—areas where we would expect high densities of ribbed mussels. Embayed marshes are typically at the heads of small, tidal creeks in very low exposure settings. Not only do we expect those areas to have fewer ribbed mussels, but lower condition ribbed mussels as well. Should this trend continue, we may see considerable decline in the services that ribbed mussels provide to those areas.

Ribbed mussels are responding to factors beyond the marsh, though it is unclear whether the response is a result of pre- or post-settlement processes. Consideration of the spatial scales at which an organism interacts with and responds to its environment have been the subject of a great deal of research in the terrestrial and even marine settings (Collinge 2009, Hitt et al. 2011, Wedding et al. 2011), but few have attempted to apply the concepts of landscape ecology to the terrestrial-aquatic ecotone (Boström et al. 2011, Isdell et al. 2015). Identification the most important factors and scales provides valuable insight into what explains observed patterns in ribbed mussel distribution and density. For ribbed mussels, the technique we have developed in this work has allowed us to create spatially explicit estimates of density across a large area that could be used for future analyses, such as projecting the impacts of land use change and marsh loss on mussel populations. Identification of any potential trends in ribbed mussel population changes within an area will provide the opportunity to take proactive steps to facilitate expansion or mitigate loss.

CONCLUSIONS

Throughout the Chesapeake Bay, ribbed mussels are predominately found within the first two meters of a marsh. Ribbed mussels are also more likely to occur in areas where there is increased exposure. In the coming half-century, we expect to see a net loss of this high-exposure marsh edge habitat due to erosion and barriers to inland migration (Bilkovic et al. 2017). Throughout Virginia, approximately 30% of all marshes fall into the exposure regime typical of the high-mussel density platform marshes of this study. These high-mussel density marshes primarily occur along rivers and bays where Bilkovic et al. (2017) estimated rates of marsh loss of 20% by 2050, which is considerably higher

than the marshes in less exposed areas (~10% estimated loss to erosion) with the lowest densities of ribbed mussels. As the rate of sea level rise and the frequency of severe weather is expected to increase for the foreseeable future (IPCC 2014, Boon and Mitchell 2015), erosion rates will also likely increase (Mariotti and Fagherazzi 2010) as marshes attempt to keep apace of sea level rise. In other estuaries where erosion rates are artificially high due to boat wakes, ribbed mussels are no longer most abundant in these high exposure areas, but rather in the narrow tidal creeks (Moody 2012). The spatial shift in higher ribbed mussel density indicates that there may be a point at which mussel recruitment and survival can no longer keep up with erosion. The potential impacts to the ribbed mussel population within the Chesapeake Bay. This study has identified trends in ribbed mussel density both within and among marshes throughout the Chesapeake Bay. Our results provide a baseline for monitoring and identifying changes to ribbed mussel populations through time and space. As an important component of salt marsh ecosystems throughout the Atlantic coast, ribbed mussels contribute to marsh persistence and valued ecosystem services. Understanding potential impacts of natural and anthropogenic stressors on ribbed mussel populations is vital to sustaining the health of our coastal ecosystems.

Beyond the Chesapeake Bay, our findings may be useful and applicable to other coastal regions throughout the ribbed mussel's range. Whether it is Barnegat Bay in New Jersey, or the Albemarle Sound in North Carolina, much of the US Atlantic Coast has been modified by human actions that have had and will continue to have an impact on marshes and their inhabitants. By determining the spatial distribution of ribbed mussels in the Chesapeake Bay through linking landscape factors to mussel density, we have

effectively established a method by which researchers and managers may assess the implications of system changes or management actions on mussel distribution and ecosystem service provision (e.g., water filtration). This method allows for the examination of ribbed mussel, or other intertidal sessile species, distribution patterns in a larger shorescape context to consider the role of factors beyond the marsh—factors that are driven by or are the result of human actions. This process thereby provides tools and insight to researchers and managers interested in setting baselines and assessing potential for change across broad spatial scales.

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TABLE HEADINGS

Table 1

Variable	Scale	K	AICc	Δ AICc
stems	local	3	110.48	0.00
water	300 m	3	116.00	5.53
forest	60 m	3	120.57	10.10
ag	300 m	3	122.65	12.18
null	N/A	2	122.76	12.28

Table 2

Model	Intercept	SE	Stems	SE	Forest	SE	Water	SE	Ag	SE	AICc	ΔAICc	wt	Adj wt
7	1.055	0.586	0.039	0.009	-0.026	0.012					108.5	0.0	0.280	0.292
6	-0.023	0.643	0.033	0.010			0.027				108.7	0.2	0.250	0.260
12	0.479	0.742	0.034	0.010	-0.018	0.014	0.018	0.015			109.7	1.2	0.160	0.167
2	0.650	0.588	0.041	0.010							110.5	2.0	0.100	0.104
14	0.997	0.646	0.039	0.010	-0.027	0.014			0.006	0.024	111.3	2.8	0.070	0.073
13	-0.032	0.789	0.033	0.011			0.027	0.014	0.001	0.023	111.6	3.1	0.060	0.063
16	0.334	0.821	0.035	0.010	-0.020	0.015	0.019	0.015	0.011	0.024	112.6	4.1	0.040	0.042
avg	0.534	0.654	0.036	0.010	-0.013	0.007	0.012	0.004	0.001	0.004				

FIGURE CAPTIONS

Figure 1 – The study area in Virginia's Chesapeake Bay. Study sites (black dots) were located along the western and eastern shores of the Chesapeake Bay.

Figure 2 – Average mussel density (± standard error) at each meter into the marsh for all sites.

Figure 3 – Average mussel density (± standard error) in platform and non-platform marshes.

Figure 4 – (a) Scales of most importance for significant variables in the mussel density or condition index models. Each circle is scaled to the distance at which the variable name above it was most important (lowest AICc value). Predicted mussel density is also overlaid for reference. (b) and (c) Representative marsh types where high (b) and low (c) densities would be expected.

Figure 5 – Predicted mussel density along the front edge (first two meters) of the marsh. Yellow areas indicate high predicted densities, while blue areas indicate low predicted densities.

Figure 6 – Condition index of mussels at each meter into the marsh.

Figure 7 – Condition index as a function of shell length at each distance into two representative marshes. Lines of best fit are provided for significant ($p < 0.05$) slopes.

Figure 8 – Shell-to-tissue ratios (STR) for each meter into the marsh.

Figure 9 – Shell-to-tissue ratios (STR) as a function of % water within a 500-m neighborhood.

Figure 1

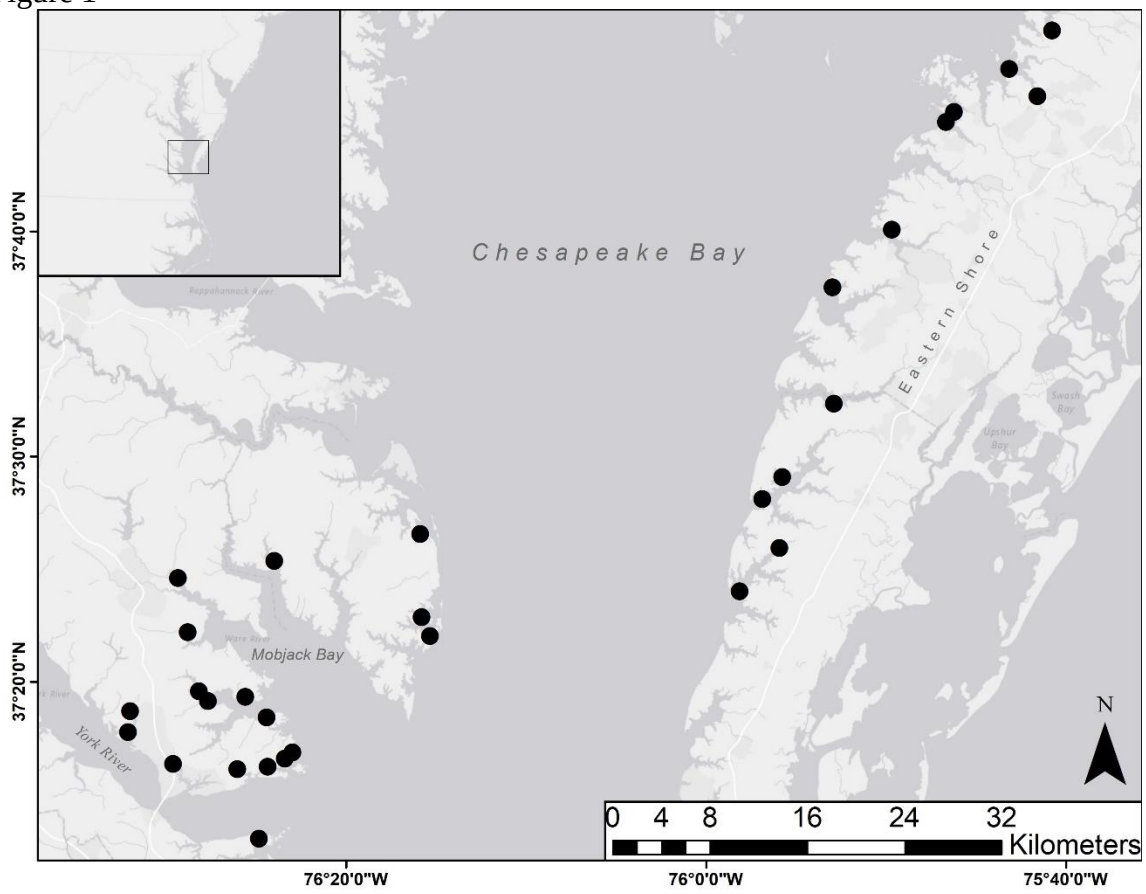

Chesapeake Bay
Eastern Shore
Mobjack Bay
York River
Rappahannock River
Upshur Bay
Swash Bay
N
0 4 8 16 24 32
Kilometers
37°40'0"N
37°30'0"N
37°20'0"N
76°20'0"W
76°0'0"W
75°40'0"W

Figure 2

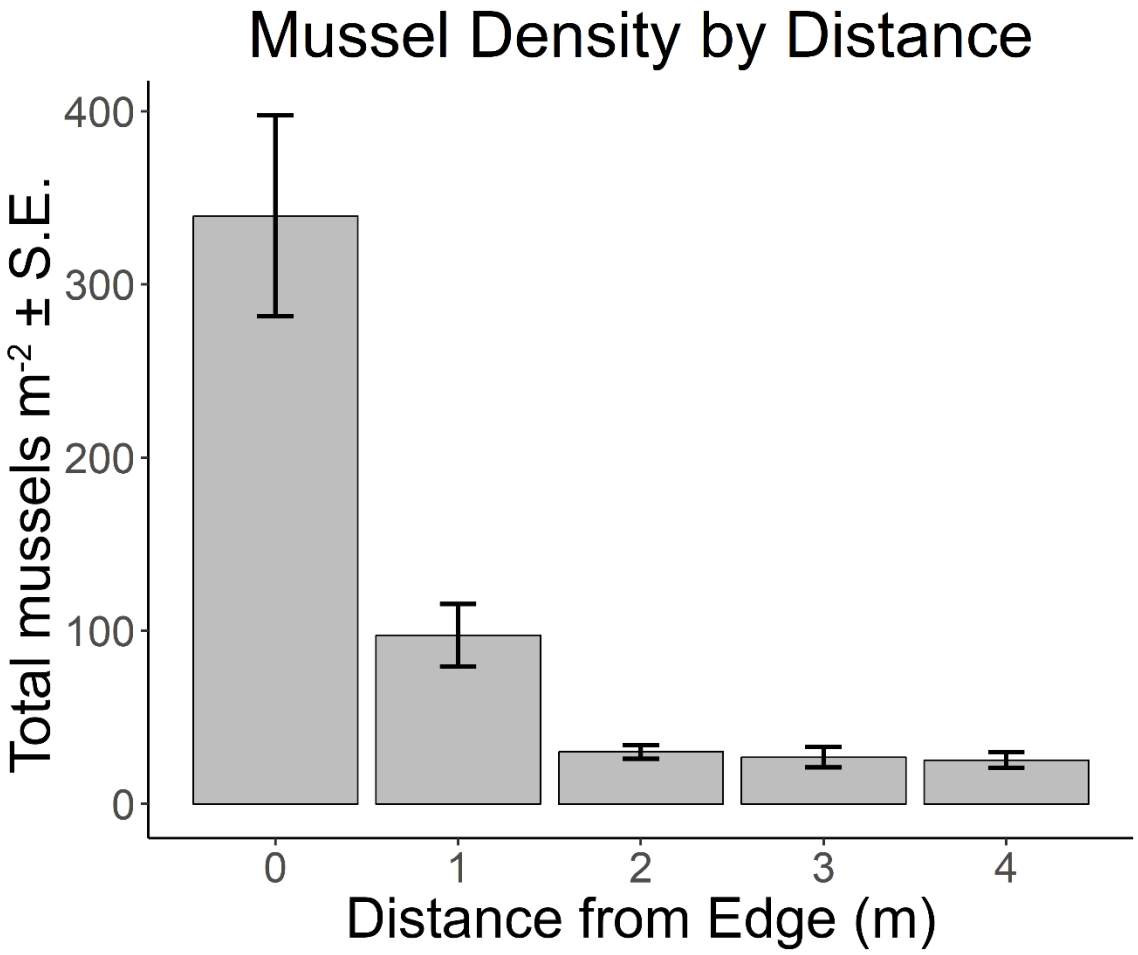

Mussel Density by Distance
Total mussels m-2 ± S.E.
400
300
200
100
0
0
1
2
3
4
Distance from Edge (m)

Figure 3

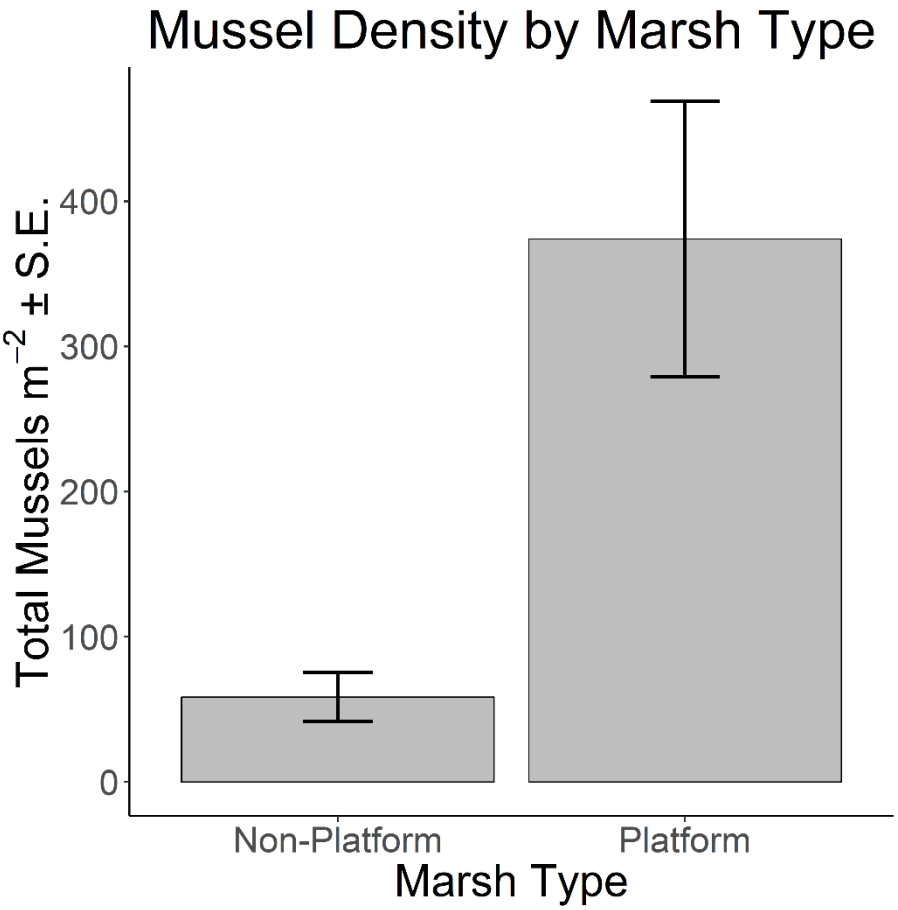

Mussel Density by Marsh Type
Total Mussels m^{-2} ± S.E.
400
300
200
100
0
Non-Platform
Platform
Marsh Type

Figure 4

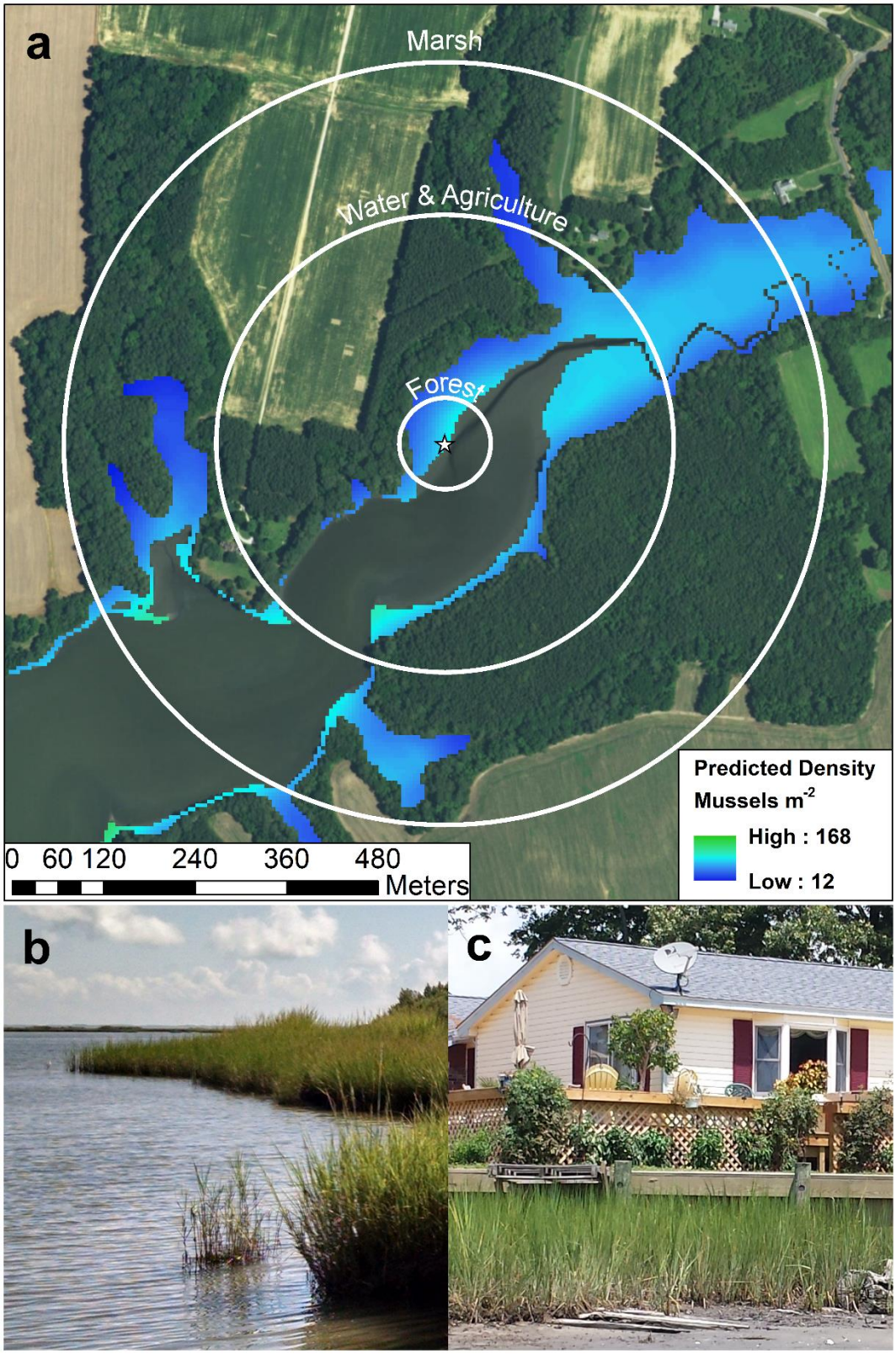

a
Marsh
Water & Agriculture
Forest
0 60 120 240 360 480
Meters
Predicted Density
Mussels m-2
High : 168
Low : 12
b
c

Figure 5

Figure 6

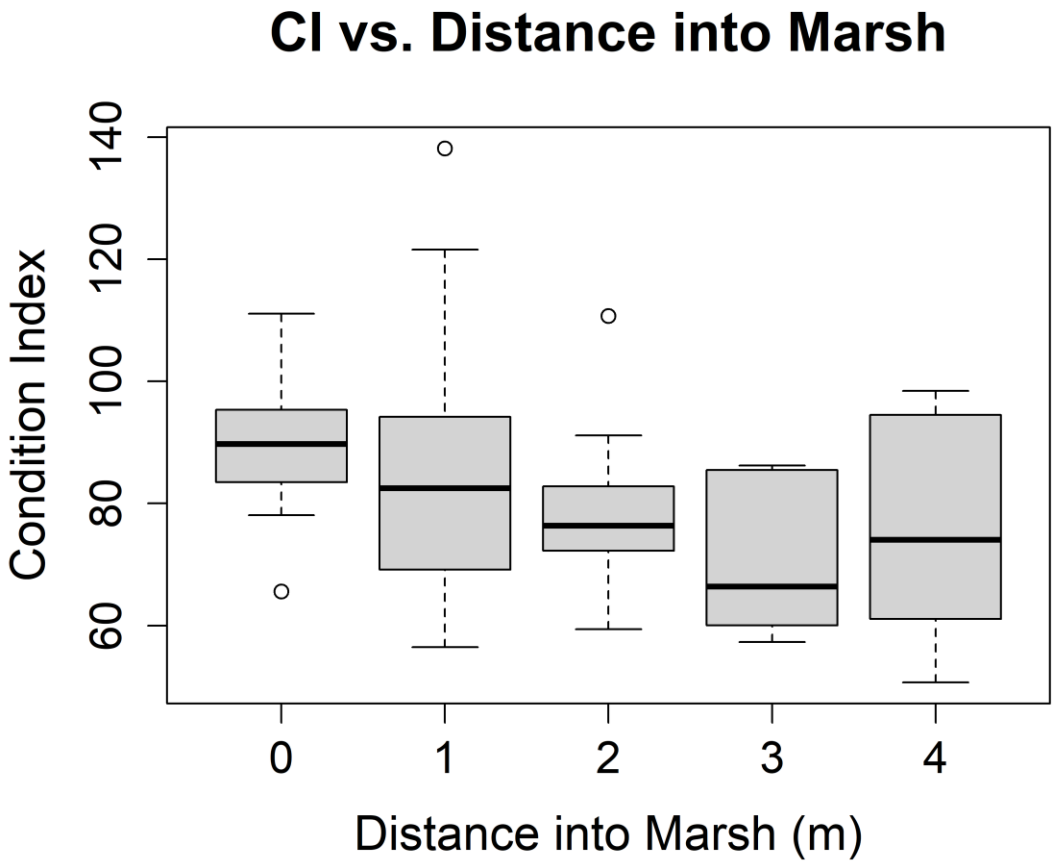

CI vs. Distance into Marsh
Condition Index
60
80
100
120
140
0
1
2
3
4
Distance into Marsh (m)

Figure 7

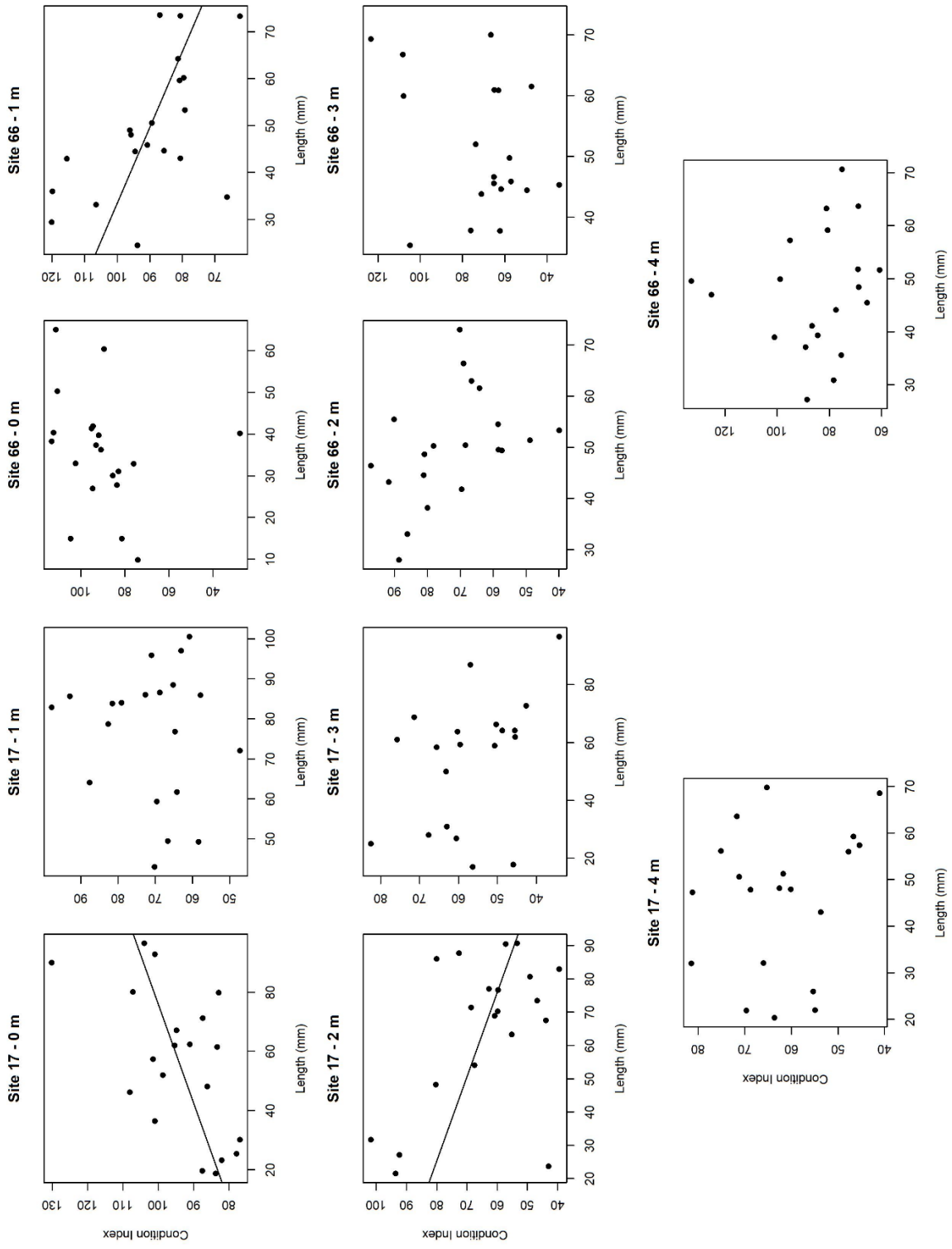

Site 66 - 1 m
Site 66 - 0 m
Site 66 - 2 m
Site 66 - 3 m
Site 66 - 4 m
Site 17 - 1 m
Site 17 - 0 m
Site 17 - 3 m
Site 17 - 2 m
Site 17 - 4 m
Length (mm)
Condition Index

Figure 8

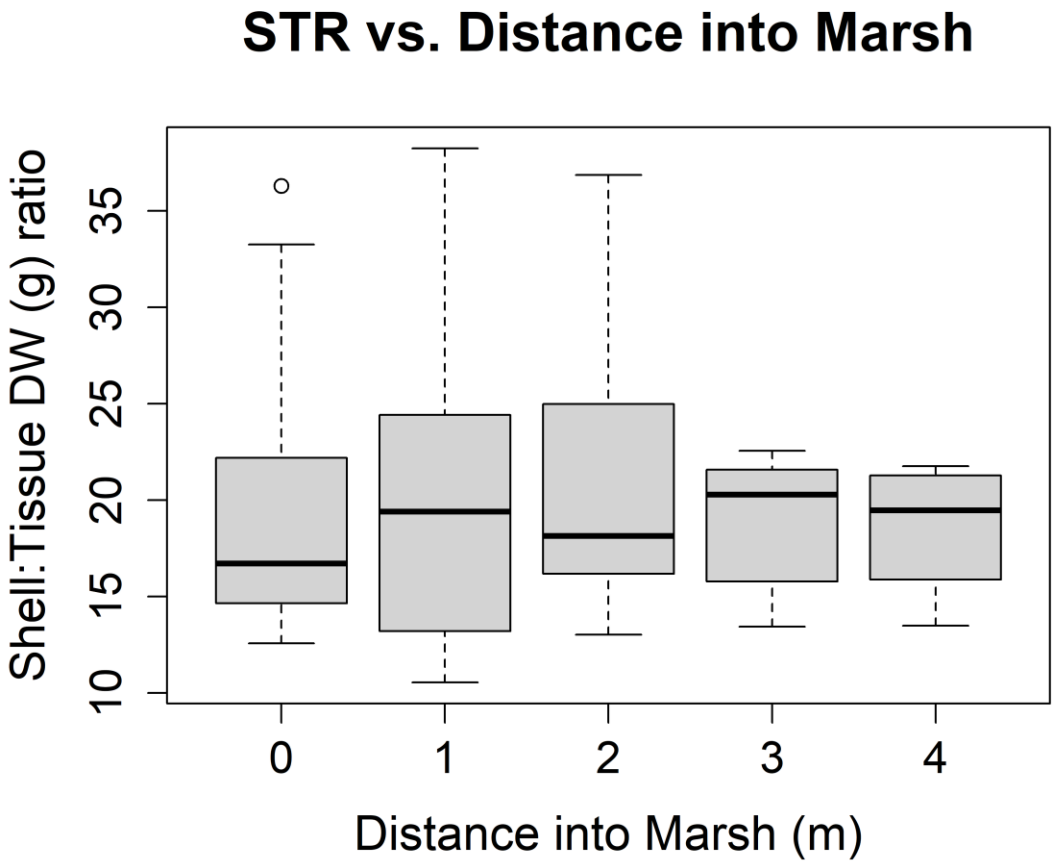
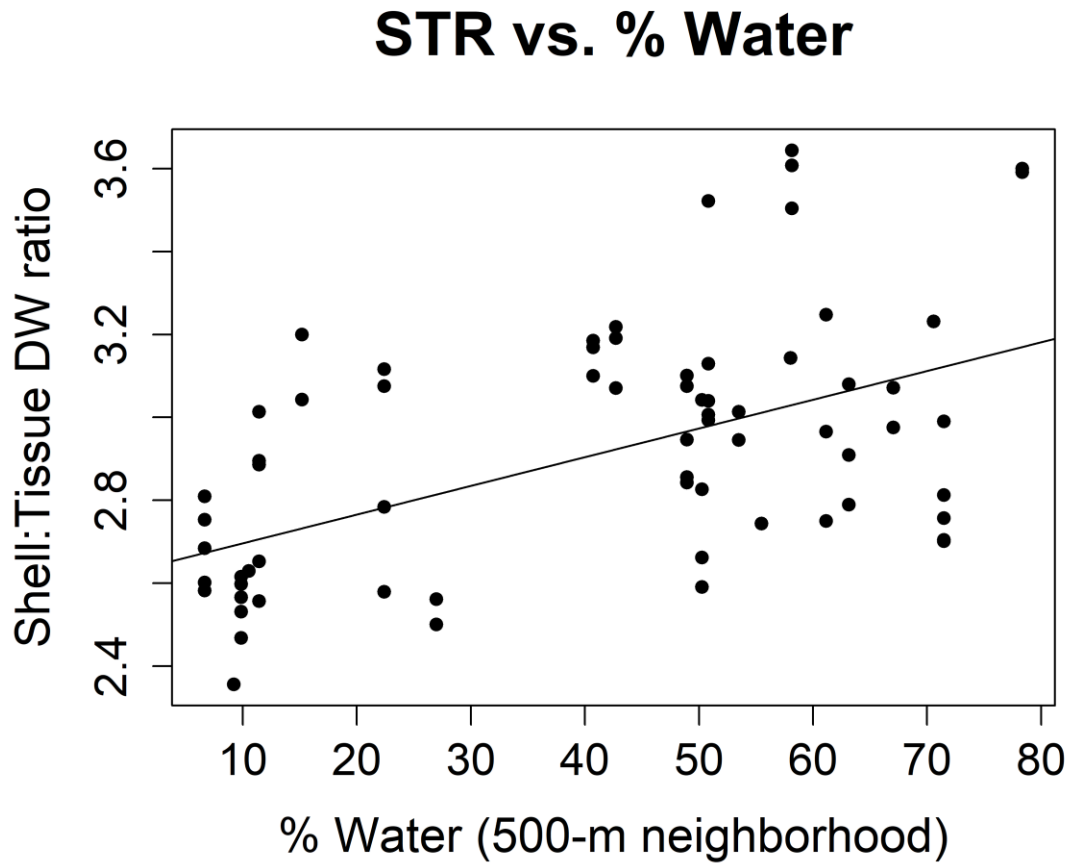

STR vs. Distance into Marsh
Shell:Tissue DW (g) ratio
10
15
20
25
30
35
0
1
2
3
4
Distance into Marsh (m)

Figure 9


STR vs. % Water
Shell:Tissue DW ratio
2.4
2.8
3.2
3.6
10
20
30
40
50
60
70
80
% Water (500-m neighborhood)

CHAPTER 3

Variable contribution of ribbed mussels *(Geukensia demissa)* to salt marsh nitrogen flux

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ABSTRACT

Ribbed mussels (*Geukensia demissa*) are filter- feeding bivalves integrated into the surface of salt marshes where they form a facultative mutualistic relationship with smooth cordgrass, *Spartina alterniflora*. As filter feeders, ribbed mussels remove particulate organic matter from the water column and assimilate it into tissue or waste. Prior studies suggest nitrogen (N) removal is elevated as a result of enhanced denitrification when ribbed mussels grow in the presence of *Spartina*. Given the influence of N on water quality issues world-wide and the potential alteration of salt marsh habitats due to sea level rise, we conducted a study designed to 1) determine how ribbed mussels influence nitrogen removal in salt marshes, and 2) identify whether N removal is modified in the presence of *Spartina alterniflora*. We collected and incubated cores in four treatments with sediment only, *Spartina* and sediment, mussels and sediment, and mussels, *Spartina* and sediment from three marshes in Chesapeake Bay, Virginia, USA. Water and particulate samples were analyzed for ammonium production, particulate removal, and nitrogen flux. We found that ammonium production was highest in treatments with mussels, but the production was offset by particulate N removal, resulting in a negative N flux in most treatments and marshes. Further, ammonium production was depressed in the treatments with both mussels and *Spartina* compared with just mussels, indicating that ammonium removal was enhanced when mussels and *Spartina* were combined. Our results further demonstrate the linkage between ribbed mussels and *Spartina* in salt marsh nitrogen cycles; how that linkage will be impacted by anticipated alteration of mussel habitat associated with ongoing, rapid sea level rise is uncertain.

INTRODUCTION

Salt marshes provide a wealth of ecosystem services. Throughout the temperate zones of the Earth, marshes are vital to local fisheries, erosion control, and water quality (Boesch and Turner 1984, Christiansen et al. 2000, Shepard et al. 2011). Despite their relatively low floral diversity (Weis and Butler 2009), marshes are among the most productive ecosystems on the planet (Lieth 1972). Salt marshes, especially, are important sites of nutrient transformation and removal (Jordan et al. 1983, Chambers et al. 1992, Giblin et al. 2013). Their location in the intertidal enhances their redox potential via cyclical exposure and inundation (Kaplan et al. 1979), resulting in increased coupled microbial nitrification and denitrification (Sousa et al. 2012). Additionally, the presence of salt marsh grasses, such as *Spartina* spp., enhances uptake of nitrogen (N) from the water column and sediments, leading to N storage in plant tissues (Deegan et al. 2012).

Removal of nitrogen from the water column, whether by plant uptake or sediment microbial activity, is a vital ecosystem service, especially in areas experiencing coastal eutrophication (Valiela and Cole 2002). Excessive use of residential and agricultural fertilizers has led to the formation of toxic algal blooms, fish kills, and dead zones throughout the world (Ingrid et al. 1996, Abreu et al. 2006). As one of the most expansive ecotones between land and water, salt marshes have the potential to capture and process a considerable portion of terrestrial N runoff before discharge to open water (Valiela and Cole 2002, Craft et al. 2008). In their classic nitrogen budget of a salt marsh, Valiela and Teal (1979) found that after accounting for denitrification, salt marshes were net sinks for nitrogen thanks to storage and denitrification, with aquatic inputs exceeding exports.

Most of the measured denitrification occurred at the waterward (henceforth front) edge of the marsh.

The front edges of salt marshes along the US Atlantic and Gulf coasts typically are populated by ribbed mussels (*Geukensia demissa* Dillwyn) (Honig et al. 2015). Throughout their range from Cape Cod, MA to southern FL, ribbed mussels form a mutualistic relationship with *Spartina alterniflora* Loisel (*Spartina* hereafter) (Bertness 1984). Mussels are initially attracted to settle and metamorphose in dense *Spartina* marshes (Franz 2001). Once metamorphosed, the *Spartina* shades mussels from the sun and protects them from predators (Bertness and Grosholz 1985). In return, the mussels anchor the sediment with byssal threads and fertilize *Spartina* with excreted ammonium and biodeposits (Smith and Frey 1985). The stable and fertile sediment promotes *Spartina* growth, improving the habitat for mussels and enhancing recruitment (Nielsen and Franz 1995), thereby continuing the cycle (Bertness 1984). Within a marsh, mussels are predominately found within the first two meters of the front edge, with decreasing abundance as distance into the marsh increases (Isdell et al. In Review, Bertness and Grosholz 1985, Honig et al. 2015, Bilkovic et al. 2017). This concentrates the mutualistic relationship at the front edge of the marsh where the most interaction with the water column occurs.

Ribbed mussels have been implicated in enhanced nitrogen processing. As bivalve filter feeders, mussels remove particulate organic matter (POM) and particulate inorganic matter (PIN) from the water column that is ingested or expelled as pseudofeces (Smith and Frey 1985, Kreeger and Newell 2001). Ribbed mussels will ingest ~50% of the N filtered from the water, and will excrete ~50% of the ingested N as ammonium—

the rest is stored in tissues (Jordan and Valiela 1982). In addition to removing particulate matter, a recent study suggests that mussels may increase the marsh's ability to remove inorganic nitrogen (Bilkovic et al. 2017). When both mussels and marsh grass were present, denitrification was dramatically increased, with a net removal of nitrogen from the system via gaseous N_2 flux. This may have been caused by increased coupled nitrification/denitrification in the sediments surrounding the ribbed mussels as a result of the water movements involved in filtration, though the authors did not conclusively identify a mechanism.

With ongoing erosion, coastal development, and sea level rise (Bilkovic et al. 2009, Boon et al. 2010, Deegan et al. 2012), the front edge of the marsh, where both ribbed mussel density and N removal are at their maximum, is subject to rapid change (Mitchell et al. 2017). Understanding how ribbed mussels influence N transformations will be important to forecast some of the impacts of continuing alteration of marsh habitat. We hypothesized that ribbed mussels were likely to facilitate more N removal in the presence of *Spartina* To that end, our goals for this study were: 1) to quantify the removal of N by ribbed mussels in a salt marsh, and 2) to identify whether N removal is modified in the presence of *Spartina alterniflora*..

METHODS

Study area and site selection

The study area was located in the southern Chesapeake Bay (Figure 1), in a region called Mobjack Bay. Salinity in this area typically ranges 17-20‰ and the vegetation along the front edge of the marshes is dominated by *Spartina alterniflora*. Sites were selected along a gradient from low exposure (a measure of how exposed a segment of

shoreline is to wave energy) to high exposure in an attempt to survey across the various physical settings present in the Chesapeake Bay. Exposure was measured using a proxy of % water within 500 m of a site. It is estimated by summing the area of water within a 500-m radius, and dividing by the area of the circle. It is designed such that a marsh along a perfectly straight shoreline along a wide river (> 500 m across) would have 50% water, while a marsh near the head of a small tidal creek would have a much lower percentage. It was shown to be an effective predictor of mussel abundance by Isdell et al. (In Review). The selected sites, Brown's Bay, Captain Sinclair, and Maryus had exposure values of 49%, 41%, and 15% water, respectively. Brown's Bay was located directly on a river, Captain Sinclair was in a sheltered part of the river, while Maryus was located in a small tidal creek.

Core collection and setup

At each site, four replicate sediment cores were collected for each of the following treatments: (1) sediment only, (2) *Spartina* in sediment (grass), (3) mussels in sediment (mussels), and (4) mussels and *Spartina* in sediment (combination), for a total of 16 cores. Each core had an internal diameter of 95.25 mm, and was 30 cm long. Cores were taken to a depth of approximately 15 cm. In the laboratory, cores were plugged with MOCAP® T3.68/3.80RD1 tapered cap plugs, and the plugs were sealed with standard vinyl electrical tape to prevent leaking. Once sealed, 500 mL of raw unfiltered water collected from the creek/river adjacent to the marsh was added to each core. Cores were placed into a large tub (to prevent leaking and toppling) at ambient temperature using random sequences generated with the random() function from the "random" package in R. The overlying water in each core was gently aerated by Pentair Aquatic Eco-

Systems® TP30 clear vinyl tubing supplied by a Pentair Aquatic Eco-Systems SL22 linear piston air pump. The remaining raw water was similarly aerated in a reservoir container located next to the tub of cores and exposed to the same environmental conditions. Cores were allowed to incubate for 18h from the time that aeration began until sampling.

Water sampling

For all sites, water samples were collected at the start of the experiment (0h) from the raw water and at 18h from each core and the raw water reservoir. Each sample consisted of 50 mL of water collected and filtered through a pre-weighed 25 mm Whatman GF/C filter using a syringe and syringe filter holder. The first 5 mL was passed through, uncollected, while the next 20 mL was collected into a clean, 20 mL scintillation vial. The remaining 25 mL was filtered through uncollected. Each filter with suspended solids was placed into a petri dish and dried with the lid ajar at 60 ℃ for 36 hours. The filtered water was refrigerated at 3 ℃ until processing.

Ammonium

Ammonium concentrations were determined using the salicylate method (Parsons et al. 1984). Absorbance values were obtained from a Spectronic Genesys 5 spectrophotometer at 640 nm, and converted to concentrations using a standard curve. Note that nitrate was also measured separately, but values were at or below the limits of detection of the test (< 1 μM) and were therefore excluded from analysis.

Particulate N

Particulate N of suspended solids was measured using a Perkin-Elmer 2400 Elemental Analyzer. Values were output as %N by weight. Total particulate N removed

from the water column was calculated as the (%N by weight / 100) * particulate weight * 10 mL * (core area^{-1}) / 18 h * 1000 mg to get units of μg N·m^{-2}·hr^{-1}. The values were then adjusted to reflect the change relative to the reservoir water at 18 h.

Nitrogen Flux

Nitrogen flux was calculated as the total amount of nitrogen produced as ammonium (μg N·m^{-2}·hr^{-1}) minus the total amount of particulate nitrogen removed (μg N·m^{-2}·hr^{-1}), both relative to the reservoir water. The production quotient was calculated as the total weight of ammonium N divided by the total weight of particulate N removed times 100. On average, mussels excrete 50% of ingested N (which is 50% of total filtered particulate N) as ammonium (Jordan and Valiela 1982). So, when mussels are present, values < 25% indicate some alternate source of N removal, potentially denitrification. Values > 25% indicate some additional source of NH_4^+, and/or less denitrification.

Core Post-processing

After the experiment, cores were broken down to quantify organic matter in the top 7.5 cm for processing. Each core was thoroughly rinsed on a 1 mm sieve to remove as much sediment as possible. Plant matter was separated into above and below-ground biomass. The below-ground biomass was further separated into live and dead tissue to distinguish live roots and rhizomes from the peat. Mussels were also removed and cleaned to remove sediment and epifauna from the shell. Organic matter from each core was frozen at -18 ℃ until further processing. All plant tissue was defrosted and dried in a convection drying oven at 60 ℃ for 72 hours until fully dried. Dried samples were weighed to the nearest 0.1 g. Mussels were defrosted and patted dry to obtain a whole weight (± 0.0001 g). Each mussel was then measured (length, height, width, ± 0.01 mm),

and shucked into pre-weighed aluminum weigh boats. Both shell and tissue were placed in a drying oven at 60 ℃ for 48 hours until fully dried. Each sample was reweighed for dry shell and tissue weights.

Statistical analyses

All statistical analyses were done in R. Two-way ANOVAs were used to identify any statistically significant ($\alpha = 0.05$) effects of site and treatment for full datasets, while one-way ANOVAs were used for within site datasets to test the effects of treatment on the response variables for each site using either the "base" or "car" packages in R. Response variables included ammonium production rates, % N by weight, and N fluxes for each core. In cases where an unbalanced design occurred as a result of sampling error (sites Browns Bay and Maryus; mussels thought to be absent from a core until post-processing revealed a concealed mussel), a Type-III ANOVA was performed. Post-hoc pairwise comparisons were done using the "pairwise.t.test" command in the "stats" package with a Bonferroni P-value adjustment.

RESULTS

Ammonium

Rates of net ammonium production were uniformly highest in the treatments containing mussels (max 850.2 $\mu g \cdot m^{-2} \cdot hr^{-1}$). In contrast, a net decrease or total removal of ammonium from the water column was observed in treatments without mussels, although rates varied by both site and treatment (Figure 2). Brown's Bay and Captain Sinclair had a significant effect of treatment on ammonium, but Maryus did not (Browns Bay: ($F_{(3,12)} = 7.46$, $p = 0.004$), Captain Sinclair: ($F_{(3,12)} = 122.9$, $p < 0.001$), Maryus:

($F_{(3,12)} = 3.16$, $p = 0.064$)). At both Browns Bay and Captain Sinclair, the mussel treatment generated significantly more ammonium than either the grass or the sediment treatments ($P < 0.05$). At Captain Sinclair, ammonium generation from the combination treatment was also significantly higher than either the grass or sediment treatments ($P < 0.05$). At all sites, ammonium production from the grass and sediment treatments were not significantly different from each other, and in all but the sediment treatment at Maryus, all ammonium was removed from the water column in cores without mussels. Although not statistically significantly different, at both Maryus and Browns Bay, net rates of ammonium production trended much lower in the combination treatments than the mussels only treatments—approaching net removal. Mussel biomass was not significantly different among treatments with mussels present within any site. When present, mussel dry weight was positively correlated with ammonium production ($P = 0.004$, adjusted $R^2 = 0.29$). Mussel biomass was significantly greater ($P < 0.05$) at Captain Sinclair than the other two sites, which were not significantly different from each other ($P = 1.00$).

Particulate Nitrogen

Treatment had a significant effect on particulate N at Brown's Bay and Captain Sinclair, but not Maryus (Browns Bay: ($F_{(3,12)} = 8.28$, $p = 0.003$), Captain Sinclair: ($F_{(3,12)} = 13.92$, $p < 0.001$), Maryus: ($F_{(3,12)} = 2.99$, $p = 0.073$)). Mussels significantly reduced particulate nitrogen at all sites when present ($P < 0.05$; Figure 2); however there was considerable variability among absolute reductions among sites and treatments. At Browns Bay and Captain Sinclair, the combination treatment significantly reduced the amount of particulate N compared to the sediment and grass treatments, and was not

significantly different than the mussel treatment at any site. At Browns Bay, the mussel treatment removed significantly more (P = 0.019) particulate N than the sediment treatment, but only marginally more than the *Spartina* treatment (P = 0.060). At Captain Sinclair, the reverse was true in that the mussel treatment removed significantly more (P = 0.002) particulate N than the grass treatment, but not the sediment treatment (P = 0.100). At Maryus, however, there were no significant differences among any of the treatments (P > 0.05).

Nitrogen Flux

Nitrogen flux primarily varied by site. Browns Bay and Maryus experienced a net removal of nitrogen from the water column, while Captain Sinclair had effectively no net flux of N (-35 ± 171 μg $N \cdot m^{-2} \cdot hr^{-1}$). The mean N flux across all treatments and all sites was -707 ± 113 μg $N \cdot m^{-2} \cdot hr^{-1}$. Total N flux did not significantly vary by treatment within each site (Browns Bay: ($F_{(3,12)} = 2.30$, $p = 0.13$), Captain Sinclair: ($F_{(3,12)} = 1.62$, $p = 0.24$), Maryus: ($F_{(3,12)} = 0.80$, $p = 0.52$); Figure 2), as treatments with mussels removed more particulate N, but also produced more ammonium. We calculated the N production quotient in treatments with mussels because ammonium production was observed only in treatments with mussels (Figure 3). Across all sites, the mean production quotient was 62.0 ± 12.6 % in treatments with mussels. A Site*Treatment two-way type-III ANOVA revealed that only site had a significant effect on the production quotient, with Captain Sinclair being significantly higher (P = 0.002) than Browns Bay. No other site comparisons differed, nor were the mussel and combination treatments different within a site (P > 0.05). Only at Browns Bay was the production quotient < 25%, where both the combination and mussels only treatment results suggested an additional source of

ammonium removal. Only the combination treatment, however, was significantly lower (one-sided *t*-test, $t = -3.29$, $P < 0.05$) than the 25% production quotient. Though not significantly different overall, the mean production quotient was lower in the combination treatments than the mussel treatments for every site. Captain Sinclair was also the only site where N production outpaced N removal. At Browns Bay, there was considerably more removal than production.

DISCUSSION

The front edges of marshes where mussels are found in highest abundance remove N from the water column, irrespective of the unmeasured, potential N removal via denitrification. Overall, removal of particulate N was nearly 5X greater than ammonium production across all sites and treatments. The ability to remove N was highly site specific. Two sites, Browns Bay and Maryus, had a net removal of nitrogen, whereas Captain Sinclair had no net N flux over the course of the experiment. Despite selecting sites along an exposure gradient, there were no clear trends towards an increase or decrease in ammonium production or particulate N removal when sites were ordered along the exposure gradient, suggesting that exposure may have very little to do with daily microbial N cycling in our system.

Mussels in the cores were clearly active during the course of the experiment as evidenced by the elevated ammonium levels and decreased particulate N levels in cores where they were present. The mussels were also observed to be open and filtering almost immediately after the water was added to the cores. The relative rates of ammonium production and particulate removal are consistent with previously published estimates for ribbed mussels (Galimany et al. 2015, Bilkovic et al. 2017). However, contrary to

expectations, neither mussels nor *Spartina* had a statistically significant effect on N flux. There were trends within sites, but those trends were neither significant nor consistent among sites. It was especially surprising that net N flux rates in the treatments with only sediment or grass were on par with those observed in the treatments with mussels. Ammonium was removed at almost identical rates in the grass and sediment treatments, which suggests that sediment and/or water column microbial processes were more important than plant root uptake, at least over the time interval examined in this study. Alternatively, it could also be that we were unable to detect a difference in the mussel-free treatments because the ammonium was completely removed by the end of the experiment, and so it becomes difficult to separate out the possible contributions of denitrification vs. uptake. However, these results still further illustrate the importance of mussels to N dynamics, given that ribbed mussels were the largest single influence on rate differences within a site.

Whereas particulate N was almost always removed at a significantly greater rate in the cores with mussels, considerable particulate N removal was measured in the treatments without mussels as well (with the exception of the Captain Sinclair site where particulate N removal was effectively zero when mussels were absent). Site level differences in particulate N removal may, at least in part, be explained by differences in sediment composition for Maryus and Browns Bay. Maryus is a very low exposure site, located along a narrow tidal creek. The sediment at Maryus was much finer, primarily a fine sand/silt with a high organic content. In contrast, the sediment at Browns Bay was almost entirely sand, with comparatively little visible organic material. The simple size differences in grain size between the two sites could account for the greater particulate N

removal seen at Browns Bay as the coarser sediments there settled out of suspension faster than the fine sediments at Maryus (Temmerman et al. 2005). Once again, the Captain Sinclair site is the exception, where sediments were much more similar to those at Browns Bay, but with more organic matter. Despite this and the increased mussel biomass at Captain Sinclair, particulate N removal was comparatively low.

The higher average production quotients observed in the mussel only treatments (Figure 3) may indicate the potential of mussels to act as net sources of dissolved N when not growing as part of a healthy marsh ecosystem. Mussels typically do not occur without *Spartina* present, but in some intertidal environments they do grow independently. In natural marshes, for example, mussels may occasionally be found in areas without *Spartina* that have been denuded by erosion, submersion, or overgrazing (pers. obs.). The extent of such impaired intertidal habitat without *Spartina* is expected to increase as climate change and sea level rise continue (Finkelstein and Hardaway 1988, Kirwan et al. 2010, Smith et al. 2013), potentially minimizing the benefits that mussels have on N removal from coastal waters. Mussels also grow without *Spartina* in the cracks and crevices among shoreline protection structures. In riprap (large pieces of rock piled along the shoreline to reduce erosion), mussels can reach fairly high densities (Bilkovic and Mitchell 2017). Given that higher densities of mussels correlated with increased ammonium production, and that areas with mussels that are not integrated into *Spartina* remove less N, the mussels living in these structures may not be as environmentally beneficial as those living in marshes. The decoupling of ammonium production from the sediment and *Spartina* uptake may alter the balance of particulate organic nitrogen to dissolved inorganic nitrogen as mussels filter out organic matter and excrete ammonium.

With less removal potential via denitrification, using ribbed mussels alternative ways to improve water quality (e.g., floating rafts of mussels) should proceed with caution, understanding that their full potential to remove nitrogen may not be met (Galimany et al. 2017).

Captain Sinclair responded markedly different from the other sites with respect to ammonium production and net N flux. Although the source of this difference is unclear, some factor or combination of factors has resulted in extreme ammonium production and reduced particulate removal. The elevated ammonium production may, at least in part, be explained by the greater mussel biomass present in the cores from Captain Sinclair. However, this only holds for a small part of the ammonium production. According to the N budget for the ribbed mussel developed by Jordan and Valiela (1982), only ~25% of the N removed from the water by filtering should be excreted as ammonium, while the rest is deposited as pseudofeces or used in cellular processes. Given that the production quotient at Captain Sinclair was in excess of 100% for both the mussel and the combination treatments, there must have either been an extra source of ammonium in the cores, or N removal was severely lacking. Alternate sources of ammonium could have included residual ammonium seeping out of the sediment left over from the semi-recent (within 2 years) construction of a fertilized living shoreline in close proximity to the natural marsh where the cores were collected. This, however seems unlikely given that ammonium levels were low in both of the treatments without mussels at Captain Sinclair. Alternatively, the mussels may have been closed for an extended period prior to the experiment causing the ammonium to build up, then be released when the mussels opened during the experiment, though evidence for this is scarce (Byrne and McMahon

1994). Heavy rains occurred the night before the cores were collected, potentially resulting in locally depressed salinity. To prevent tissue damage, which occurs at or below 8‰ (Shumway and Youngson 1979), the mussels may have closed during this period, even while submerged. They would have remained closed or at least unable to excrete for the 3 hours immediately prior to sampling given that sampling occurred at low tide. Also notable is that particulate N removal rates at Captain Sinclair were not commensurate with mussel biomass. Despite having significantly greater mussel biomass than Maryus, the particulate N removal rates were relatively similar overall for treatments with mussels at Captain Sinclair and Maryus. This may suggest that the mussels were not filtering as well at Captain Sinclair as at the other sites.

This study, though somewhat limited in scope, provides several insights into the influence of ribbed mussels on N removal in salt marshes. While we were not able to directly measure coupled nitrification/denitrification, we believe it was the most likely explanation for decrease in ammonium concentration at Browns Bay. NO_x was also at or below detection limits in all of the cores and raw water for all of the treatments, which is particularly surprising given that the conditions should have been conducive to nitrification. Alternatively, assimilation of NO_x by autotrophs was rapid enough that it was occurred as quickly as ammonium was oxidized. This may indicate a thriving benthic and/or pelagic algal community (Grant and Turner 1969), neither of which was directly measured in this study. Despite these limitations, we have clearly demonstrated that mussels are important ammonium contributors in salt marsh systems where they remove particulate N. Through their excretions, mussels support primary productivity of both *Spartina* (Bertness 1984) as well as benthic microalgae (Pfister 2007). This in turn

supports primary and secondary consumers, thereby establishing a strong link between the role of ribbed mussels in the N cycle and in the ecosystem.

CONCLUSIONS

Salt marshes are important locations of nitrogen transformation and removal, and ribbed mussels are clearly an integral part of these processes. We have demonstrated that ribbed mussels produce ammonium against a backdrop of microbial removal and plant uptake. Further, while this work focused on particulates and ammonium, it is also important to remember that a roughly equal amount of N is produced by the mussels as ammonium is stored in their tissues (Jordan and Valiela 1982). This provides short-term storage, and makes the N available to secondary consumers. Additionally, while this study clearly shows that particulate N removal outpaced ammonium production, the fate of the particulate N is not fully known. It is unclear how much will be resuspended and flushed out with the next tide versus how much is removed via denitrification or anammox (Koop-Jakobsen and Giblin 2009, Sousa et al. 2012). Of the particulate N that is stored in the sediments, much of that is likely to reenter the water column when the front edge of the marsh erodes or is submerged as sea level rises (Craft et al. 2008), making the length of time that N is stored dependent upon the erosion rates along that stretch of shoreline. It is clear from this work and that of Bilkovic et al. (2017) that the ribbed mussel/*Spartina* complex facilitates nitrogen transformation and removal. As marshes continue to move landward and/or disappear, we need to understand how the constituent components of marshes interact to provide the ecosystem services on which we rely. Increased sampling efforts and direct measurements of denitrification may provide a clearer picture of the intertwined roles that ribbed mussels and *Spartina*

alterniflora play in nitrogen removal from the water column, and how those roles may change as climate change, sea level rise, and human development continue to modify the coastal environment.

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FIGURE CAPTIONS

Figure 1 – Map of the study area where the star in the inset map shows the location of the study, and the points in the larger map show the individual marsh locations.

Figure 2 – Bar plot of the ammonium (top), particulate N (middle), and N flux (bottom) rates for each treatment per site in this study. The error bars are ± SE, and the units for all rates are in $\mu g\ N \cdot m^{-2} \cdot hr^{-1}$.

Figure 3 – Bar plot of the production quotient (ammonium production/particulate removal*100) for treatments with mussels at each site. The numbers over the bars indicate the treatment mean, the error bars are ± SE, and the units are percentages.

Figure 1

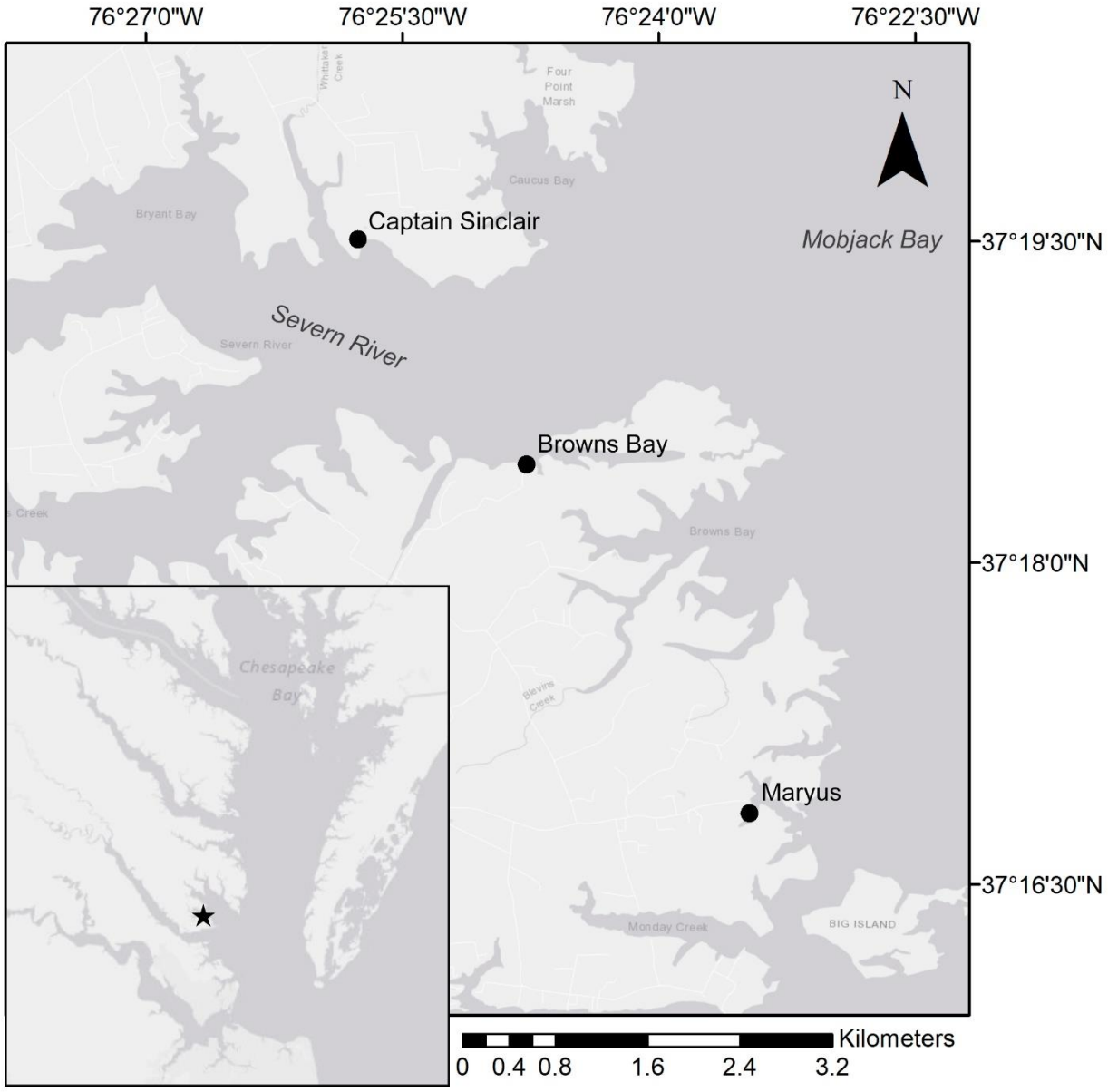

76°27'0"W
76°25'30"W
76°24'0"W
76°22'30"W
N
Four Point Marsh
Whittaker Creek
Caucus Bay
Bryant Bay
Captain Sinclair
Mobjack Bay
37°19'30"N
Severn River
Severn River
Browns Bay
Browns Bay
37°18'0"N
Chesapeake Bay
Blevins Creek
Maryus
37°16'30"N
Monday Creek
BIG ISLAND
Kilometers
0 0.4 0.8 1.6 2.4 3.2

Figure 2

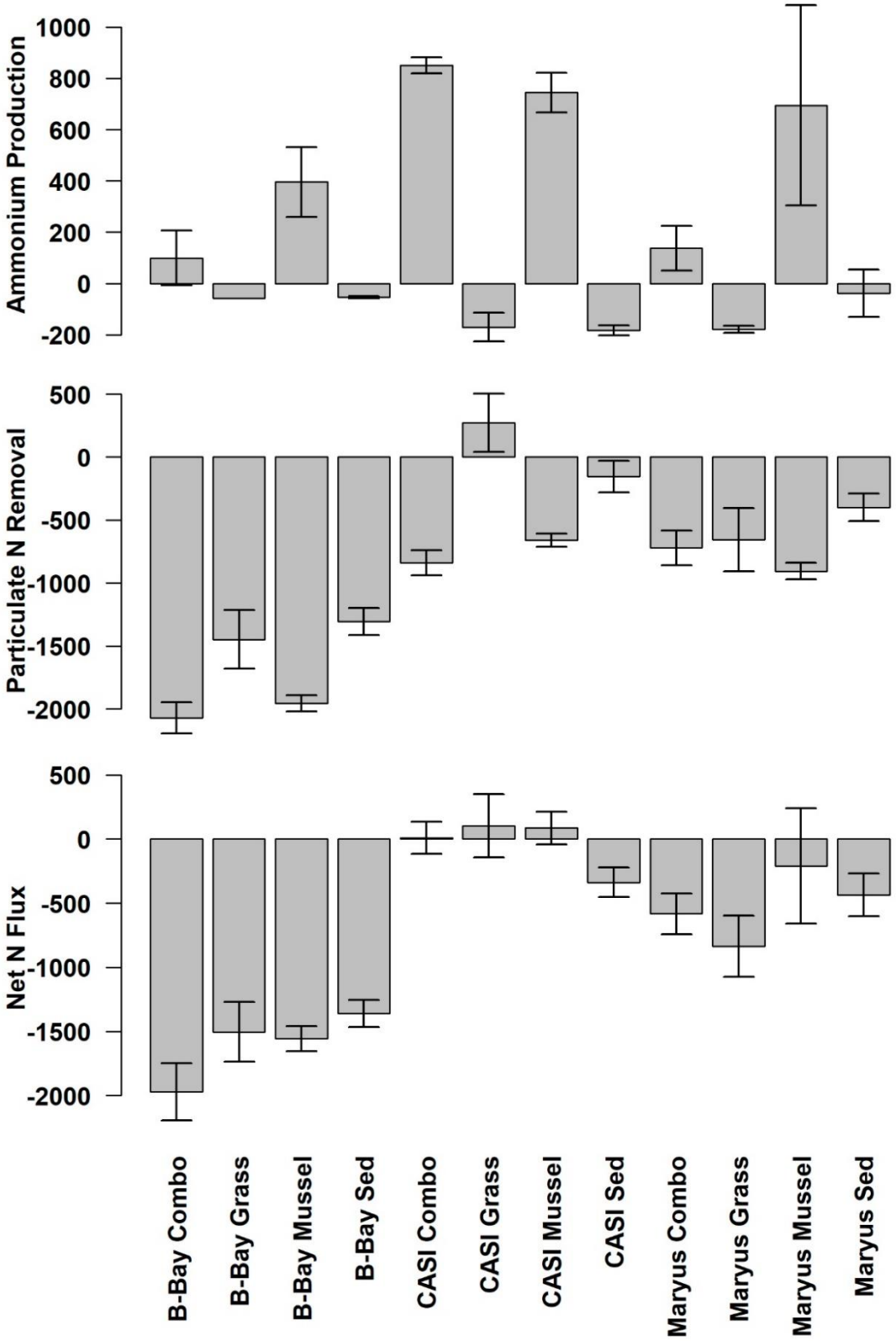
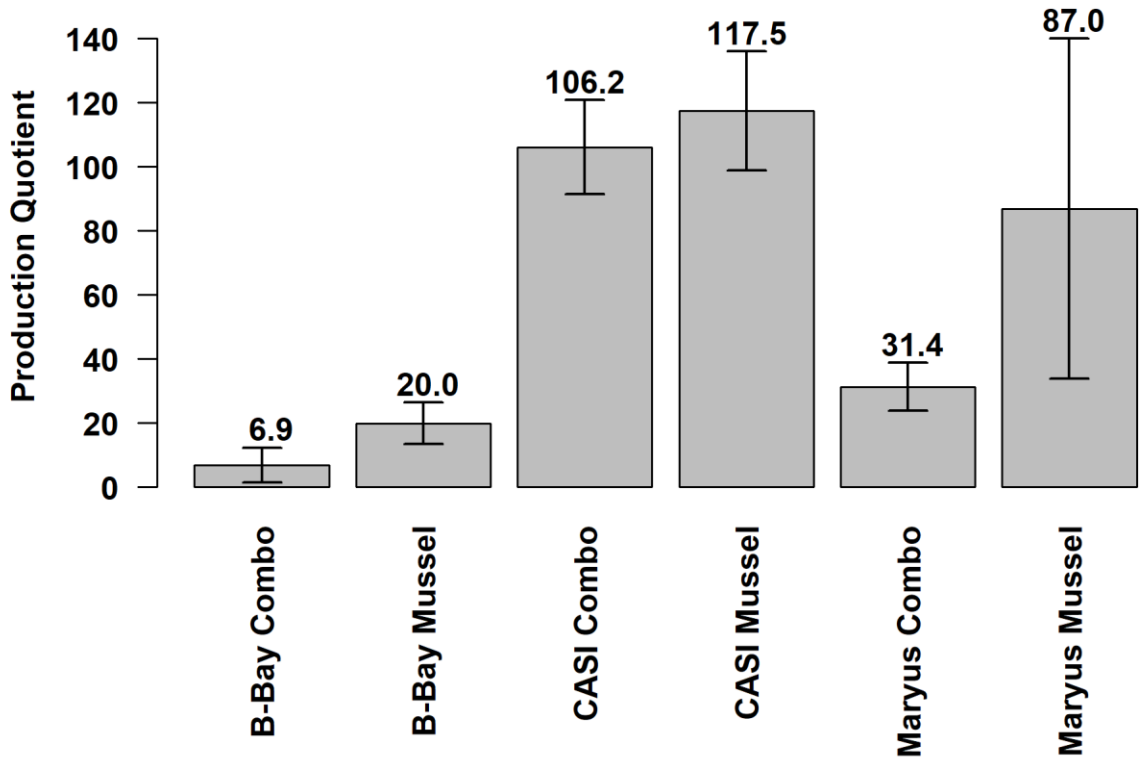

Ammonium Production
1000
800
600
400
200
0
-200
Particulate N Removal
500
0
-500
-1000
-1500
-2000
Net N Flux
500
0
-500
-1000
-1500
-2000
B-Bay Combo
B-Bay Grass
B-Bay Mussel
B-Bay Sed
CASI Combo
CASI Grass
CASI Mussel
CASI Sed
Maryus Combo
Maryus Grass
Maryus Mussel
Maryus Sed

Figure 3


Production Quotient
140
120
100
80
60
40
20
0
6.9
20.0
106.2
117.5
31.4
87.0
B-Bay Combo
B-Bay Mussel
CASI Combo
CASI Mussel
Maryus Combo
Maryus Mussel

CHAPTER 4

Inequitable redistribution of ribbed mussels (*Geukensia demissa*) and their ecosystem services due to sea level rise

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ABSTRACT

Salt marshes provide a wealth of ecosystem services that are vital to the health, safety, and economic wellbeing of their proximal waters and human communities. Despite their importance, salt marshes and their inhabitants are being displaced by climate change and human development along the coastline. One such inhabitant, the ribbed mussel (*Geukensia demissa*), is an important bivalve filter feeder that forms a mutualistic relationship with smooth cordgrass *Spartina alterniflora* along the US Atlantic Coast. Ribbed mussels stabilize the marsh, remove particulate matter from the water column, and promote denitrification, thereby improving local water quality. In the Chesapeake Bay, where historically high nutrient inputs have resulted in chronic eutrophication and subsequent government mandated improvement targets, ribbed mussels are important in mitigating nutrient inputs and improving local water quality. In order to quantify the potential for ribbed mussels to improve local water quality, we compared the current and projected future (2050) spatial distributions of ribbed mussels in Chesapeake Bay using the Mussel Distribution Model (MDM), assuming an intermediate 0.58 m sea level rise based on the best available sea level rise models for the region. We found that ribbed mussel abundance remained relatively static (3.6% decrease), but there was a large redistribution of mussels and their ecosystem services throughout the Chesapeake Bay. Mussel losses in most watersheds were offset by very large gains in just a few agricultural watersheds with extensive marsh and minor armoring. The greatest losses occurred in urban watersheds with extensive armoring and narrow fringing marshes lost to coastal squeeze. Observed gains were primarily a result of marsh fragmentation and conversion of marsh interior to edge—an unsustainable mechanism for long-term

maintenance of mussel populations. These shifts in distribution will be important considerations to management efforts to meet water quality goals and enhance tidal wetlands.

INTRODUCTION

Along the salt marshes of the United States Atlantic Coast, ribbed mussels, *Geukensia demissa* (Dillwyn 1817), form a mutualistic relationship with *Spartina alterniflora* (Loisel.; henceforth *Spartina*). *Spartina* provides habitat for the ribbed mussel in several ways. First, *Spartina* stems promote particle trapping by acting as baffles in the water (Leonard and Croft 2006). Ribbed mussel larvae are sufficiently small (Baker and Mann 2003) to be influenced by the viscosity dynamics that strongly influence the behavior and transport of particles with low Reynolds numbers in water (Scheltema 1986, Vogel 1994). Like large sediment grains, ribbed mussel settlement is facilitated by the low flow environment created by the *Spartina* marshes. Once settled, the shade provided by an extensive *Spartina* canopy reduces thermal and desiccation stress, which enhances mussel metamorphosis and survival (Bertness 1984). Ribbed mussels burrow into the sediment of salt marshes where they attach to the roots, rhizomes, and stems of the *Spartina* using their byssal threads. By attaching themselves, they also bind the sediment and reduce erosion, thereby improving the stability of the marsh (Bertness 1984, Bertness and Leonard 1997). The mussels filter considerable amounts of water (Wright et al. 1982, Kreeger and Newell 2001, Bilkovic and Mitchell 2014), excrete ammonium and deposit nutrients on the surface of the marsh in their feces and pseudofeces (Jordan and Valiela 1982). These excretions, in turn, fertilize the sediment, which promotes the growth of *Spartina* resulting in a positive feedback loop. More *Spartina* stems mean more shade and more particle trapping, thus promoting mussel recruitment, survival, and vertical accretion of the marsh.

Within salt marshes, ribbed mussels are capable of providing a wealth of ecosystem services. These filter feeders are capable of clearance rates on par with oysters (Kreeger and Newell 2001), and effectively remove a wide size range of particulate matter. Ribbed mussels are exceptional in their ability to filter bacteria from the water column, making them especially valuable for improving water quality issues (Wright et al. 1982, Kreeger and Newell 2001). Through the process of filtration, ribbed mussels ingest particulate N, which they subsequently assimilate to their tissues, and deposit excess particulates and waste on the surface of the marsh (Jordan and Valiela 1982). Early evidence indicates that mussels also improve denitrification when they are grouped with *Spartina*, resulting in higher N removal from the system than either could achieve separately (Bilkovic et al. 2017a). Stabilizing and fertilizing the sediment increases the resilience of the marsh (Angelini et al. 2015, 2016) by reducing erosion and promoting shoot growth (Bertness 1984), thereby enhancing the marshes ability to protect the upland during storm events (Schuerch et al. 2013). Mussels sequester nutrients from both terrestrial and aquatic sources, making the nutrient available to their numerous predators such as blue crabs (*Callinected sapidus*, Rathbun 1896), mud crabs (*Panopeus herbstii*, H. Milne Edwards 1834), raccoons (*Procyon lotor*, Linnaeus 1758), and shorebirds (Seed 1980, Brousseau 1984, Bertness and Grosholz 1985, Lin 1990, Eichholz et al. 2009). Mussels, however, are not homogeneously distributed across the marsh surface. Throughout much of their region, mussels are densest on the front (waterward) edge of the marsh where they can achieve numbers in excess of 5,000 individuals per m^2 (Bertness and Grosholz 1985, Bilkovic et al. 2017a).

Along the front edge of the marsh, we (Isdell et al. in review) have previously identified several factors that influence the distribution of mussels throughout the study area. These factors included *Spartina* stem density, % water within a 300-m radius of a point along the shoreline (used as a proxy for exposure; referred to as exposure henceforth), % forest within a 60-m radius of a point along the shoreline, and % agriculture within a 300-m radius of a point along the shoreline. The link between mussels and *Spartina* is well established, as indicated above. Throughout Virginia, mussel densities are greatest along the edge of more exposed marshes, such as those along rivers or large tidal creeks. This may be an effect of greater food availability, larval supply, tidal flushing of sediments, or a combination of these three factors. Forested land cover within a close proximity is negatively correlated with mussel density along the edge, and we hypothesized two reasons for this. The first reason is that forested land cover in close proximity to marshes often have a steeper slope than the preceding marsh, which results in a type of natural coastal squeeze—the process by which the front (waterward) edge of the marsh is receding at a greater rate than the back (landward) edge is moving inland due to sea level rise (Pontee 2013). The second reason is that dense forest cover right next to a narrow fringing marsh may shade the *Spartina*, resulting in decreased growth (Chen et al. 2005) and subsequent recruitment of ribbed mussels. Agriculture has a very slight positive impact on mussel density, a result that we attributed to variation in local farming practices throughout the study area, with some practices benefiting mussels and others harming. This Mussel Distribution Model (MDM; Isdell et al. in review), allowed us to identify that high exposure marsh edges with dense *Spartina* and minimal nearby forest are high-quality mussel habitat.

Unfortunately, marshes around the world are rapidly changing in response to sea level rise (SLR), erosion, and human development. As the planet continues to warm as a result of anthropogenic releases of greenhouse gasses, land ice is melting and flowing into the oceans, raising the sea level (IPCC 2014). As this process continues and accelerates (Boon 2012), salt marshes will struggle to maintain their vertical position within the tidal frame (Kirwan et al. 2010). While there are mechanisms for marshes to keep apace of sea level rise (SLR), in many regions, the rate of SLR is expected to exceed the rate that marshes can sustainably accrete, resulting in marsh loss (Mitchell et al. 2017). Erosion is also playing a key role in the transformation of marshes through coastal squeeze. Coastal squeeze can be the result of both natural and human causes (Doody and Williams 2004, Torio and Chmura 2013). Natural causes include an increasing slope at the landward edge of the marsh, which decreases the potential rate of inland migration. Humans can also engineer sudden changes in slope/elevation at the back of a marsh by building shoreline protection structures such as riprap or bulkhead. These structures are designed to reduce erosion, but also create a physical barrier that impedes landward migration of the marshes. Eventually, marshes caught between these structures and a rising sea are likely to disappear entirely.

Like many urban estuaries around the world, the Chesapeake Bay has long been plagued by water quality issues caused by human disturbance and activities (Kemp et al. 2005). Decades of intense agricultural and urban runoff into the numerous tributaries of the Chesapeake Bay resulted in a highly eutrophic system and the development of an annual dead zone (Diaz and Rosenberg 2008). The loss of wildlife and commercially valuable species, in addition to the poor water quality, led to the establishment of several

agreements between the states within the Chesapeake Bay watershed and the US Environmental Protection Agency (EPA) to reduce the input of nutrients from a variety of sources (Linker et al. 2013). Due, in part, to the limited success of these agreements and the continued water quality issues of the Bay, in 2010, the EPA established Total Maximum Daily Loads for each sector of the Bay which requires states to meet the goals established within (US Environmental Protection Agency 2010).

Accounting for the water quality improvement capacity of wild populations of shellfish is important for accurate assessments and planning to meet water quality goals. To date, very few management plans have incorporated standing or projected stocks of wild shellfish as water quality mediators despite their proven potential (for example, see USACE 2014). Oysters have long been promoted for their water quality improvement potential (Kellogg et al. 2014), and numerous studies have documented their ability to remove particulate organic and inorganic matter from the water column, improving visibility and reducing nutrients (Grabowski et al. 2012, Ermgassen et al. 2013). Ribbed mussels, in contrast, have received very little attention for their ability to remove nutrients and improve water quality on a large scale. One of the limiting factors for this is the lack of understanding of the spatial distribution of ribbed mussels within an estuary. With only limited published estimates of ribbed mussel abundance in any large system (i.e., beyond the scale of a marsh; see Honig et al. 2015 and Bilkovic et al. 2017), we cannot take the next step of estimating their overall contribution to water quality. As such, we have the following objectives for this study: 1) to simulate future mussel abundance and distribution under projected sea level rise in the lower Chesapeake Bay, 2) to compare current and modeled future mussel distribution, and 3) to estimate changes to

mussel-mediated nutrient removal and water filtration because of mussel population shifts, and the implications for water quality in the Bay. We hypothesize that ribbed mussel abundance in the Chesapeake Bay is likely to decrease as marshes are also expected to decrease in the future due to drowning and coastal squeeze (Mitchell et al. 2017). We expect these losses to be greatest in urban areas where extensive armoring and high exposure have accentuated the conditions necessary for coastal squeeze, and that ribbed mussel-mediated ecosystem services will also be similarly impacted.

METHODS

Study area and site selection

Our study area was inclusive of the *Spartina*-dominated salt marshes within Virginia waters of the Chesapeake Bay, a microtidal estuary with a tidal range of ~1m. In this region, salinities are variable throughout the year, but range from near euhaline at the mouth of the Bay, to fresh at the uppermost tidal extents. We restricted our study to marshes within ribbed mussel physiological tolerances, $\geq 8‰$ (Lent 1969). The total shoreline within the study area was ~6,700 km.

Mussel model

The current distribution and abundance of mussels along the front edge of the marsh (first two meters perpendicular to the water) was determined using the MDM developed by Isdell et al. (in review). Several surveys have suggested that the vast majority (~85%) of mussel biomass within a marsh resides in the front edge of the marsh (Isdell et al. In Review, Bilkovic et al. 2017a), and so modeling the edge will provide the greatest insight into potential changes in mussel distribution. Spatial application of the MDM was completed in ArcMap v. 10.4.1 (ESRI 2017) using the raster calculator tool.

Land use/land cover (LULC) data was derived from the VGIN 1 m Land Cover dataset (2016; https://bit.ly/2HwWWcy), and resampled to 5-m resolution using the "Resample" tool and majority technique. Moving window analyses were run using the "Focal Statistics" tool at the corresponding scale (e.g., forest at 60 m) for each LULC type. *Spartina* stem density was held constant at a mean density (224 stems m^{-2}; derived from surveys conducted in Isdell et al. In Review) throughout the study area to allow for spatial application throughout the study area.

Future marsh and mussel extent

Future marsh extent was derived from work done by Mitchell et al. (in prep). To set a timeframe for shifts in elevation in the tidal frame, a sea level rise projection curve based on data from Sewell's Point, Virginia tide gauge was used, which suggests a 0.58m increase in sea level by 2050 (Boon and Mitchell 2015). Sea level rise projections vary minimally across the Virginia portion of the Chesapeake Bay (Ezer and Atkinson 2015), and Sewell's Point is considered representative of overall trends. The vegetated tidal marsh frame in the Chesapeake Bay falls in the elevation range between mean sea level to highest astronomical tide, considered to be a 0.61m envelope in this analysis across the Chesapeake Bay, Virginia (Mitchell et al. in prep). Appropriate elevations encompassed in the tidal marsh frame projected for 2050 were selected from a lidar-based digital elevation model (DEM; https://goo.gl/2djptg). Land use data in the projected 2050 tidal frame were selected from the VGIN 1m Land Cover dataset (2016). For the purposes of this study, marsh migration was permitted into all pervious surfaces other than actively managed forests or turf on the assumption that these areas would be protected with some form of structure to prevent loss. Further, marsh migration was restricted from moving

beyond existing barriers such as shoreline armoring. Erosion was incorporated into the future extent by multiplying known annual erosion rates reported in Hardaway et al. (2017) by 32 (the number of years between 2018 and 2050) to estimate where the shoreline would be in 2050. We believe that this approach gives the best available approximation of future potential mussel habitat for the study area.

Mussel abundances in 2050 were estimated by adjusting predictive factors to reflect future conditions and applying the MDM to the projected future marsh distribution under sea level rise. The water layer was recreated to incorporate the erosion and landward migration of the marshes. The other predictors (*Spartina* density, agriculture, and forest) were held constant because there are no spatially accurate estimates of how these factors will change by 2050. All area below the future tidal envelope estimated by Mitchell et al. (in prep) was considered to become subtidal and categorized as water.

Zone of inference

We selected 12-digit hydrologic unit codes (HUCs) as our zones for spatial inference. The 12-digit HUCs provide convenient regions that primarily focus on small rivers or large tidal creeks rather than political boundaries. This allows for a large, yet still localized approach to our analysis. We modified the shapefile provided by USGS (Henley 2006) by splitting HUCs that spanned both shores of the major rivers (James, York, and Rappahannock Rivers) down the center of the channel. Our modeled estimates of mussel distribution fell within 84 HUCs, which were selected for further summaries. Within each HUC, we summarized the LULC data for agriculture, forest, impervious surface, and wetlands that fell within the 2050 tidal envelope, as well as the whole HUC.

The total abundance of mussels for present and 2050 estimates, as well as the total area of marsh edge habitat at each time was summarized using ArcGIS 10.4.1.

Statistical analyses

We developed a conceptual model (Figure 2) using relative proportional changes to both mussel density and the amount of edge within watersheds. Relative changes were calculated as the proportion of loss or gain of mussels in a watershed by 2050 relative to the number of mussels in 2018, and were used to eliminate issues of varying watershed size. Absolute changes were calculated by subtracting the number of mussels in 2018 from the number of mussels in 2050. We created a standard four quadrant design with relative mussel change on the y-axis and relative edge change on the x-axis. We added a 1:1 diagonal line to the figure. Data that falls along this line would indicate that for every 1% increase in edge, mussels would also increase by 1%. Areas above the line will have a high mussel-to-edge ratio (MER), while areas below the line will have a low MER. The figure is divided such that if a watershed has a positive mussel change above the diagonal line, it will mean that mussels had a greater proportional increase than edge (sections A1 and A2) indicating an increase in higher quality edge habitat. If a watershed loses mussels but is still above the diagonal line (section A4), that will mean that fewer mussels were lost than edge habitat, indicating that proportionally more low-quality edge was lost than high-quality edge. Below the diagonal line, the opposite is true, such that if a watershed has greater mussel loss than edge loss or gain (sections B4 and B3), or that if both mussels and edge habitat increased (section B1), the edge increases were in lower quality mussel habitat and as such mussels did not increase as much as edge habitat. Each watershed was assigned a group based on the conceptual model, and mussels and LULC

were summarized for each. All statistical analyses were completed using R (R Development Core Team 2011).

Ecosystem Service Calculations

We used literature derived estimates for mussel filtration, biodeposition, and denitrification rates (Table 1). We assumed 12 hours per day for filtration and biodeposition on the basis of average marsh edge inundation frequency, and 24 hours per day for denitrification. All rates were dependent on biomass (g dry tissue weight). For our calculations, we used the median dry tissue weight per mussel (0.26 g) derived from >1,000 mussels collected from around the study area by Isdell et al. (in review), multiplied by the predicted number of mussels per m^2. All rates were transformed to expected annual contribution per watershed. When available, we used seasonally-referenced rates for each corresponding season (e.g., Spring rate · 90 days). We selected two regions, one predominately urban and one predominately agricultural, from the Chesapeake Bay Program (CBP) segments (https://bit.ly/2I8raE1) to compare our estimates of service changes and nitrogen removal capacity with the established targets of the TMDLs for those set forth by the EPA.

Assumptions

The work presented here is dependent upon several assumptions. The first is that marshes in the Bay will not be able to keep up with the rate of relative sea level rise, and that we can accurately predict where the resulting changes in distribution will occur. Kirwan et al. (2010) suggest that sediment starved estuaries experiencing rates of relative SLR > 5 mm are especially at risk, thereby increasing the risk of converting marsh to unvegetated subtidal habitat. The extensive marshes along the Blackwater River, just

north of Accomack County, are visibly fragmenting due to rapid relative SLR (Schepers Lennert et al. 2017). Based on the above evidence, we feel that an elevation-based approach will provide reasonable approximations of future marsh change. The next assumption in model development is that we can accurately predict the location and abundance of mussels, both at present and in the future. The MDM was shown to explain 62% of the variation in an independent dataset of mussel abundance in the region. Given that ecological models often fail to exceed an R^2 of 0.5, we believe the MDM to be an acceptable tool for predicting mussel density at a location. We also assume that shoreline armoring will remain static in the future. This is an obviously erroneous assumption, but necessary given our inability, at present, to predict where shoreline armoring is most likely to occur in the future (Isdell 2014). Our inability to predict future shoreline armoring expansion will most likely result in an underestimate of ribbed mussel losses in those areas where shoreline armoring will be constructed.

RESULTS

Among the 80 watersheds examined in this study, total mussel abundance decreased from 805 million in 2017 to 776 million in 2050. Losses were observed in 53 of the watersheds (mean = -3.94 ± 0.69 million mussels) and gains were observed in 27 (mean = 6.68 ± 1.93 million mussels), with a range of -28 to 44 million mussels. Much of this increase is attributable to increased habitat availability (marsh edge) as a result of the shifting tidal frame and resulting fragmentation of large marshes (Figure 3) and widening of tidal channels, resulting in a greater exposure.

Using our conceptual model for classifying relative mussel change compared to relative edge habitat change (Figure 4), there were a total of 16 watersheds in A1, 6 in

A2, 17 in A4, 5 in B1, 2 in B3, and 34 in B4. These groups saw proportional changes in mussels of 94%, 9%, -35%, 25%, -10%, and -41%, respectively. Overall, the watersheds ranged from a 75% loss of mussels to a 265% increase in mussels, while edge habitat changes ranged from a 75% loss to a 193% increase. Spatially, relative decreases were greatest in the southern and western portions of the study area, and were concentrated in more urban watersheds, while increases were concentrated in the northeast corner of the study area in a predominately agricultural area. Mussel losses are mediated by retention or even expansion of high quality marsh edge habitat despite net edge loss (A2 and A4), and increases are enhanced by more high quality edge habitat when edge increases (A1) (Table 2). Compared to the group B areas (n=41), group A areas have less forest and armoring, and more marsh. At the watershed level, the high MER group (group A) was characterized by considerably more marsh and less armoring and forested land cover than the low MER group (group B; Table 2).

The distribution of absolute changes in mussel abundance varied considerably from the distribution of relative changes. Absolute change, similar to the relative change, indicated an overall average low-level loss of mussels throughout the study area. However, while most of the study area lost mussels or had modest gains, one area in particular, Accomack County on the Eastern Shore of Virginia (northeast corner of the study area), showed massive gains. In just seven watersheds, there were ~140 million mussels gained between 2018 and 2050, which accounted for 78% of all mussel gains throughout the study area. This region is characterized by large, extensive marshes, and very little shoreline armoring. The future scenario showed substantial fragmentation of the marshes throughout this region, resulting in the conversion of interior to edge (Figure

3). In contrast, in areas with some of the greatest losses (red colors on Figure 5), narrow fringing marshes predominate, and these urban watersheds shorelines are often heavily armored.

Translating the previously described changes in mussel abundance to changes in ecosystem services shows considerable regional differences in how local water quality may be impacted (Figure 6). On average, regions that gain mussels will filter an additional 15.2 ± 4.4 $GL \cdot y^{-1}$ (range 0.1 – 100.3 $GL \cdot y^{-1}$), produce 418.8 ± 121.0 kg $N \cdot y^{-1}$ (range 2.8 – 2,766.5 kg $N \cdot y^{-1}$) of additional biodeposits, and remove an additional 196.6 ± 56.8 kg $N \cdot y^{-1}$ (range 1.3 – 1,298.8 kg $N \cdot y^{-1}$) via denitrification (Figure 5). In contrast, regions that lose mussels will filter 9.0 ± 1.6 $GL \cdot y^{-1}$ (range -63.6 – -0.2 $GL \cdot y^{-1}$) less water, produce 247.2 ± 43.0 kg $N \cdot y^{-1}$ (range -1,755.5 – -4.7 kg $N \cdot y^{-1}$) fewer via biodeposits, and remove 116.1 ± 20.2 kg $N \cdot y^{-1}$ (range -824.2 – -2.2 kg $N \cdot y^{-1}$) via denitrification. The direct link between mussel abundance and services provided means that the spatial redistribution of those services follows suit. Urban watersheds were most severely impacted, while agricultural watersheds, particularly those in Accomack County, benefited the most.

To compare changes in nitrogen removal capacity between the present and future mussel populations to the TMDL targets for two of the CBP segments, we chose the Lynnhaven River (LYNPH) as our urban setting, and the upper Eastern Shore (POCMH) as our rural/agricultural setting. Compared to the 2025 TMDL goal for N inputs, mussels along the edge of marshes are currently able to remove 1.1% and 5.2% of nitrogen loading in the urban and agricultural segments, respectively. However, by 2050, mussels along the marsh edge will only be able to remove 0.5% of the inputs to the urban system,

while expansion in the agricultural system will lead to 10.0% removal of all N input (Table 3).

DISCUSSION

Despite little overall change in mussel numbers, local changes in future mussel population densities may be dramatic. The redistribution of mussels with a net decrease nearly everywhere and concurrent increase in Accomack County results in a massive aggregation of the Bay's ribbed mussels in a comparatively small region. In fact, we predict that this one county will contain nearly 38% of all of Virginia's mussels by 2050, despite only having 13% of the land area within the study region. The negative impact of this redistribution will be greatest in urban watersheds (those in red on Figure 5) where the losses will be the greatest. The loss of mussels in urban watersheds, in concert with rising populations (Theobald 2010), is likely to have an overall negative impact on the health of the local waters. Despite only removing ~1% of total anthropogenic N inputs to the system at present (Table 3), ribbed mussels likely still play an important part in maintaining ecosystem health and integrity in these watersheds through their other ecosystem services such as filtration and marsh stabilization.

The conversion of extensive marsh interior to edge habitat through retreat and fragmentation was a driving force for mussel expansion in the simulation, and responsible for the largest gains predicted in Accomack County. Subtle elevation variations in the extensive marshes of Accomack County should allow for some regions of the current interior marsh to remain above water after the 0.58 m sea level rise forecast by 2050. Much of this new edge habitat will be in the form of marsh islands, thereby maximizing potential edge. Marsh islands, however, are among the most susceptible to

sea level rise as inland migration is not an option, leaving only vertical accretion to help them maintain their position in the tidal frame. Other studies have identified that marsh islands in one tributary of Virginia exhibited the greatest loss of all configurations in the past few decades (Mitchell et al. 2017). As such, breaking extensive marshes into marsh islands is a clearly unsustainable mechanism for long-term maintenance of the ribbed mussel population in Virginia.

Mussel population outcomes, driven by marsh change, ultimately depend on the changes in amount and type of edge habitat. Small increases in high quality edge habitat can offset relatively larger losses in low quality edge habitat. As a result, the type of marsh and the nature of the adjacent upland land cover determine outcomes. The most striking differences that we noted were between the high MER group and the low MER group. Mussels did better in places with extensive marshes (~ > 50%) and very little armoring (< 18%; Table 2), which allowed for both inland migration of the marshes, as well as the fragmentation mentioned above. Even when edge habitat was lost within the high MER group, mussels were able to expand in some watersheds due to relative increases in high quality edge habitat, or if there was a net loss of mussels, the losses weren't as great as edge losses due to retention of high quality edge habitat. Forested land cover was also considerably lower in the new tidal envelope of the high MER group than the low MER group. We believe that there are two likely explanations for this. The first is that forested land cover is typically associated with a higher relief area, and may indicate a natural topographic barrier to inland migration, resulting in natural coastal squeeze. The second reason is that the MDM has a negative relationship between abundance and forested land cover within a 60-m radius. We hypothesized that when marshes are in

close proximity to forested land cover, shading may occur, resulting in reduced *Spartina* growth and therefore lower quality habitat Isdell et al. (In review). Forested land cover may also be greater at the heads of creeks where energy is lower, and mussel densities are also low.

The projected changes in ecosystem services are non-trivial. Despite a removal capacity of 10% or less of the total nitrogen inputs to a system, the first two meters of a marsh represent a very small amount of the area in these watersheds. This results in a dense concentration of N removal potential and filtration capacity, making the ribbed mussel/*Spartina* partnership along the marsh edge highly valuable per unit area for these services. Meeting TMDL goals is vital to the future health and sustainability of the Chesapeake Bay (Linker et al. 2013). We believe that successful strategies for achieving these goals should include consideration of the natural capital available in the form of bivalve filter feeders, and ribbed mussels in particular.

The assumptions that we made for this study are most likely to result in an underestimate of mussel change by 2050. By assuming that all pervious surface that will be within the future tidal envelope will be suitable habitat for ribbed mussels almost certainly overestimates how much habitat will be available in the future. Further, our necessary assumption of zero shoreline armoring growth fails to account for the additional coastal squeeze resulting in marsh loss that armoring growth will cause. This will be especially true in areas of greater exposure, making the loss of these habitats even more acutely felt given the greater densities of mussels found in higher exposure settings. Shorelines in densely populated areas are also most likely to be armored for property protection (Kittinger and Ayers 2010), making these losses even greater in urban areas

which have historically struggled to reduce nutrient inputs to healthy levels in adjacent waters. Therefore, we believe that our assumptions have resulted in a fairly conservative estimate of change, and expect that the actual change may be considerably larger.

The primary mechanism for loss of mussels in the study area was coastal squeeze on fringing marshes, while gains were a result of fragmentation and conversion of interior marsh to edge habitat. Marshes all around the world are experiencing the impacts of coastal squeeze, and the subsequent loss of ecosystem services (Torio and Chmura 2013). The impacts of armoring go beyond the loss of the adjacent marsh to impact whole ecosystems. Studies have documented the shifts in community structure and species presence when as little as 10-25% of the shoreline is armored (Silliman and Bertness 2004, Bilkovic et al. 2006, Bilkovic and Roggero 2008, DeLuca et al. 2008, Isdell et al. 2015) within a 1-km radius. Because of these impacts, researchers and managers alike have been recommending an alternate to traditional shoreline stabilization techniques: living shorelines. Living shorelines, as defined by Bilkovic et al. 2016, are, "created or enhanced shorelines that make the best use of nature's ability to abate shoreline erosion while maintaining or improving habitat and water quality." These features may or may not include an engineered stabilization structure, such as rip rap, but must include a living component, such as a marsh or oyster reef. Unlike traditional methods, living shorelines that use engineered stabilization structures in concert with a planted marsh place the natural features behind the structure, which allows for inland migration. These living shorelines are thought to perform many of the same ecosystem services that natural marshes provide, but the extent and magnitude is largely dependent on individual project specifications and construction (Bilkovic et al. 2017b). Utilizing living shorelines as

mitigation strategy to offset the expected losses in urban settings may be a useful and prudent tool. Although early research has indicated lackluster ribbed mussel recruitment to these systems (Bilkovic and Mitchell 2017), research into optimizing these management strategies to incorporate ribbed mussels is ongoing in both the Chesapeake Bay and Delaware Bay.

CONCLUSIONS

Ribbed mussels are an integral part of the US Atlantic coast saltmarsh ecosystem. The mutualistic relationship between ribbed mussels and *Spartina* promotes the stability and functionality of these ecosystem service-rich habitats. Given their aggregation along the front edge of the marsh, where SLR and erosion will have their biggest impacts, understanding where and how mussel populations are most likely to change in the future provides key insights into their resulting loss or gain of services. In systems like the Chesapeake Bay where water quality is poor due to anthropogenic inputs, and relative SLR is high, these changes in mussel abundance and distribution are likely to have noticeable impacts on the surrounding environment. Our study has demonstrated that the ribbed mussel population will not respond homogeneously throughout the Chesapeake Bay, with clear areas of gains and losses. Preparing for and adapting to the impacts of climate change and sea level rise must involve a comprehensive understanding of how changes in existing natural capital will impact our ecosystem restoration goals.

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TABLE HEADINGS

Table 1 – Ecosystem service rates used for mussel service contributions. In the "Rate" column, Sp is the Spring rate, Su is Summer, and F is Fall/Autumn.

Table 2 – Summary of future tidal envelope land use/land cover, and mussel and edge habitat change by change index group. Watersheds that fall into groups above the 1:1 line will have a high mussel-to-edge ratio (MER), and watersheds that fall into groups below the line will have a low MER. The specific group that a watershed falls into will tell us something about how the future edge habitat is distributed among high and low-quality edge relative to the current distribution. All units are in percentages.

Table 3 – Summary of the relative contribution of ribbed mussels currently and in 2050 to the 2025 TMDL targets for two CBP segments. Units are in kg $N \cdot yr^{-1}$, and the percentages reflect what proportion of the TMDL goal that ribbed mussels are estimated to remove.

Table 1 -

Service	Source		Rate	Units
Filtration	Galimany *et al.* (2013)		2.00	$L \cdot h^{-1} \cdot g^{-1}$
Biodeposition	Jordan and Valiela (1982)	Sp	$29.8(wt)^{0.839}$	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$
		Su	$78.0(wt)^{0.856}$	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$
		F	$24.5(wt)^{0.770}$	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$
Denitrification	Bilkovic *et al.* (2017)		12.92	$\mu g\ N \cdot h^{-1} \cdot g^{-1}$

Table 2 –

Change Index	Agriculture	Forest	Marsh	Impervious	Armoring	Edge	Mussel
A1	7.00	22.66	59.26	1.71	6.35	54.97	93.47
A2	0.91	18.98	61.59	2.79	13.06	-15.58	9.24
A4	1.79	25.56	49.00	4.05	17.02	-43.79	-35.18
B1	2.85	33.37	34.50	2.37	37.10	68.96	24.64
B3	5.94	38.64	39.43	1.45	25.38	16.10	-9.64
B4	2.38	40.90	32.73	3.30	22.78	-29.37	-41.02

Table 3

Segment	TMDL Goal	Current Mussel Contribution	2050 Mussel Contribution
Urban	209,662	2,317 – 1.1%	982 – 0.5%
Agricultural	125,431	6,489 – 5.2%	12,491 – 10.0%

FIGURE CAPTIONS

Figure 1- The study area was located in Virginia's portion of the Chesapeake Bay. Watershed boundaries used for this study are outlined in black. State boundaries are indicated by a broken black line.

Figure 2 – Conceptual figure relating proportional changes in mussels to proportional changes in edge. The diagonal line indicates a 1:1 mussel-to-edge ratio (MER). Watersheds that fall above the line have a high MER, while those that fall below the line have a low MER.

Figure 3 – Projected mussel densities (mussels m^{-2}) along marsh edges in two regions of the study area. The left side (A and C) are from an extensive marsh in Accomack County, while the right side (B and D) are from an urban watershed in Virginia Beach. The top of the figure (A and B) shows mussel density estimates in 2018, while the bottom half (C and D) is for 2050. The highest densities are shown in green, while the lowest densities are shown in blue.

Figure 4 – Map of the study area showing watersheds classified by their assigned change index group. Greens indicate a high MER, and red-yellow indicates a low MER.

Figure 5 – Mussel abundance by watershed for 2018 (A), 2050 (B), and the absolute change between them (C). In panels A and B, greens are lower abundances and blues are higher abundances. In panel C, blues indicate gains, and reds-yellows indicate losses.

Figure 6 – Bar plot of ribbed mussel ecosystem services, summarized by watersheds with mussel gains vs. losses.

Figure 1

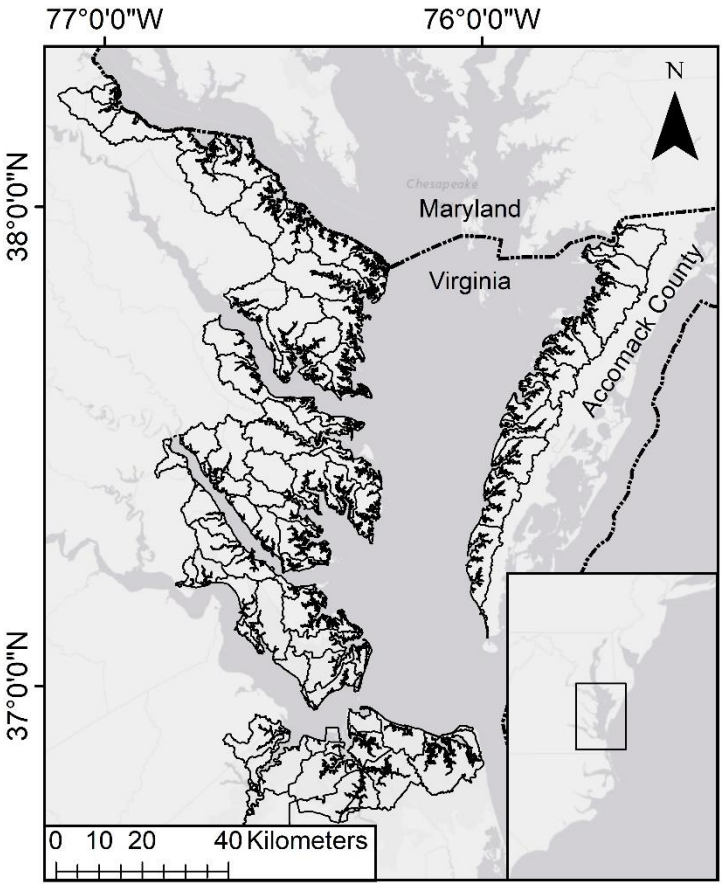

77°0'0"W
76°0'0"W
38°0'0"N
37°0'0"N
N
Maryland
Virginia
Accomack County
0 10 20 40 Kilometers

Figure 2

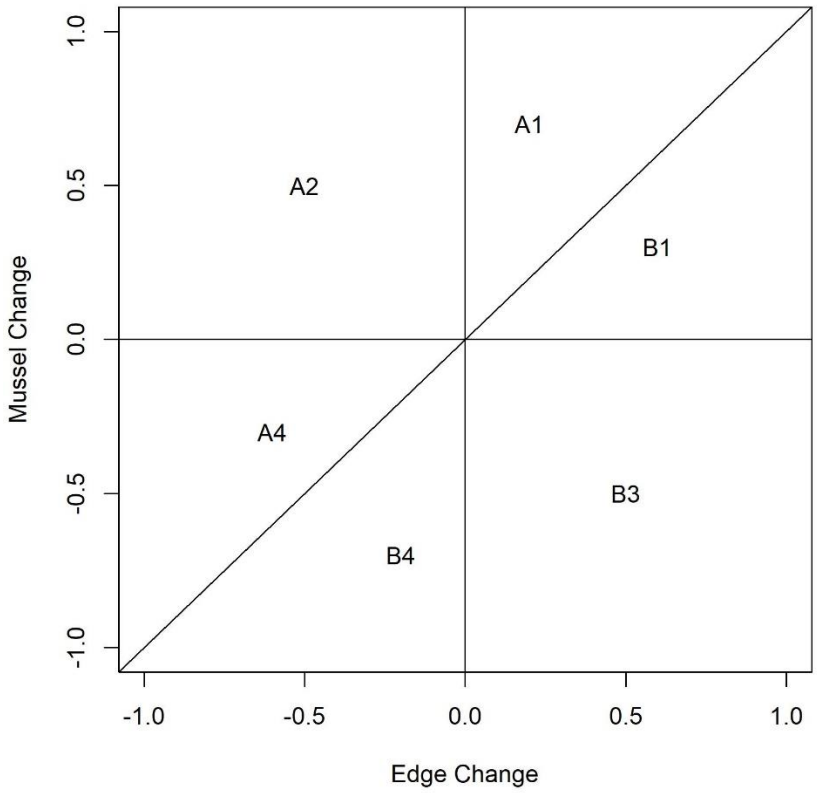

A1
A2
B1
A4
B3
B4
Mussel Change
Edge Change
1.0
0.5
0.0
-0.5
-1.0
-1.0
-0.5
0.0
0.5
1.0

Figure 3

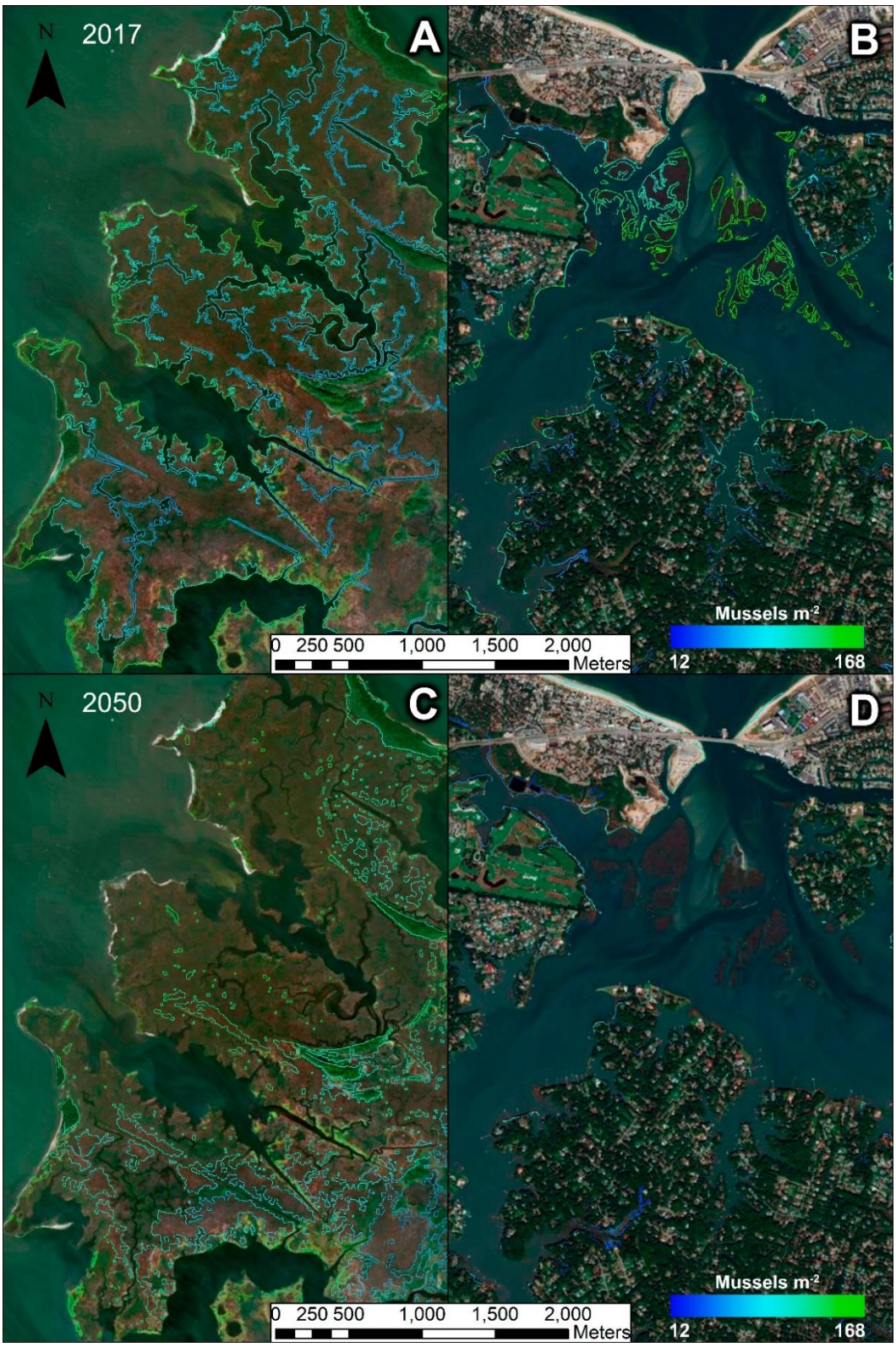

N
2017
A
B
0 250 500 1,000 1,500 2,000
Meters
Mussels m-2
12
168
N
2050
C
D
0 250 500 1,000 1,500 2,000
Meters
Mussels m-2
12
168

Figure 4

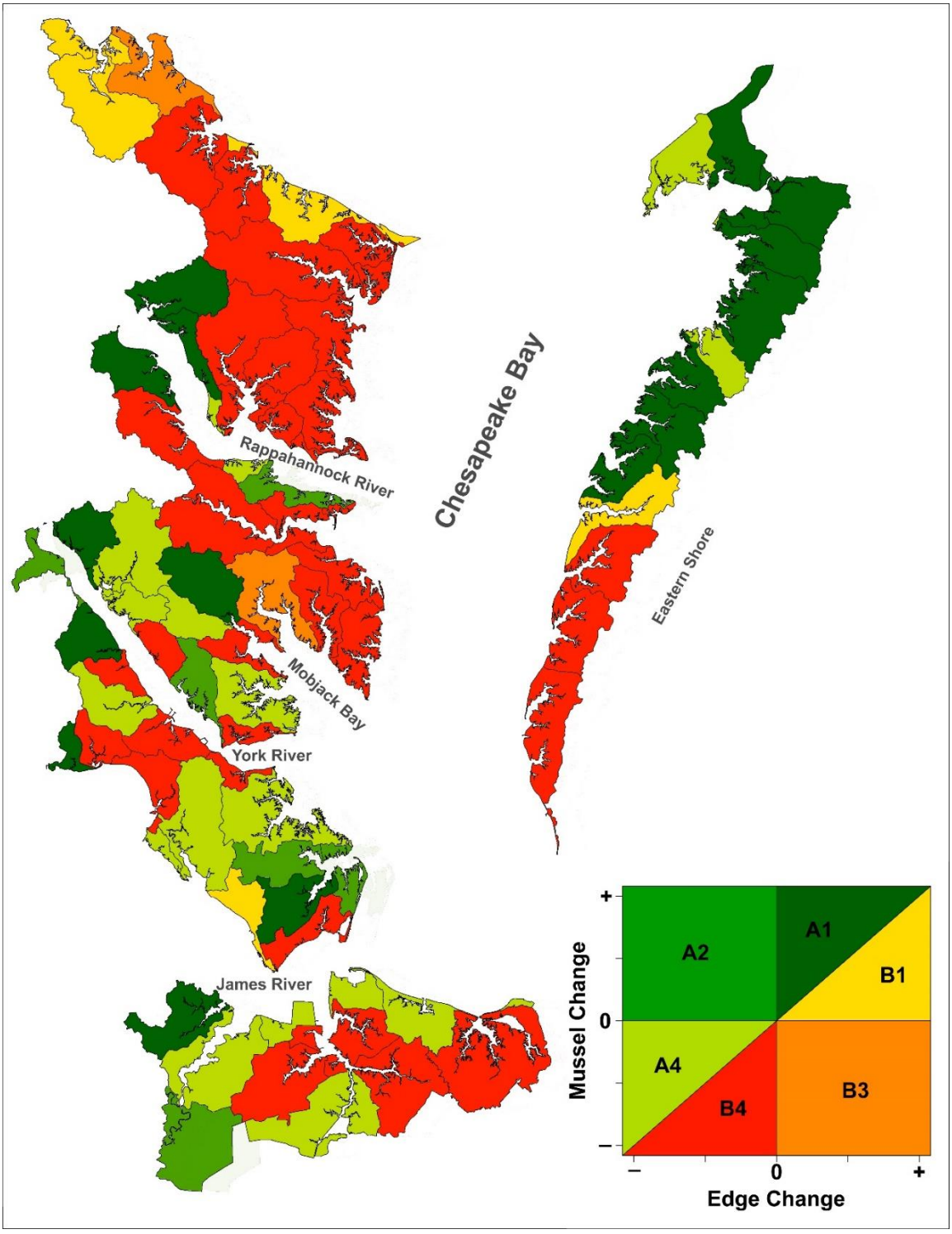

Chesapeake Bay
Rappahannock River
Mobjack Bay
York River
James River
Eastern Shore
A1
A2
A4
B1
B3
B4
Mussel Change
Edge Change
+
0
–
+
0
–

Figure 5

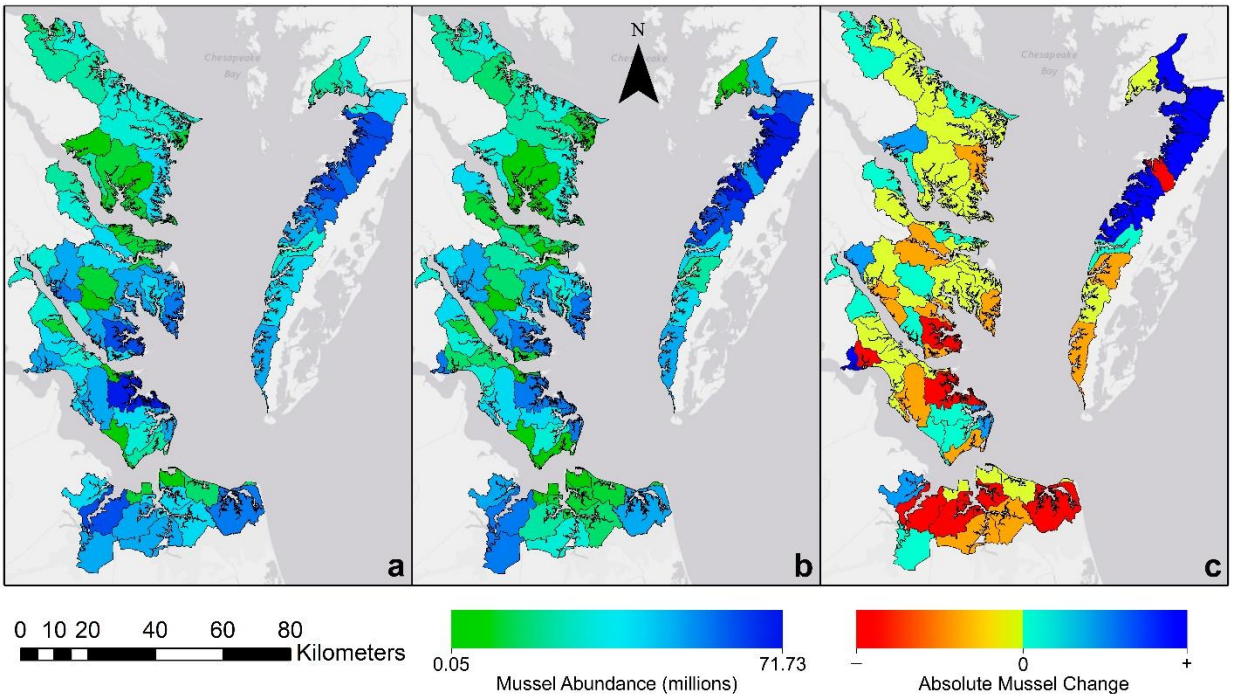
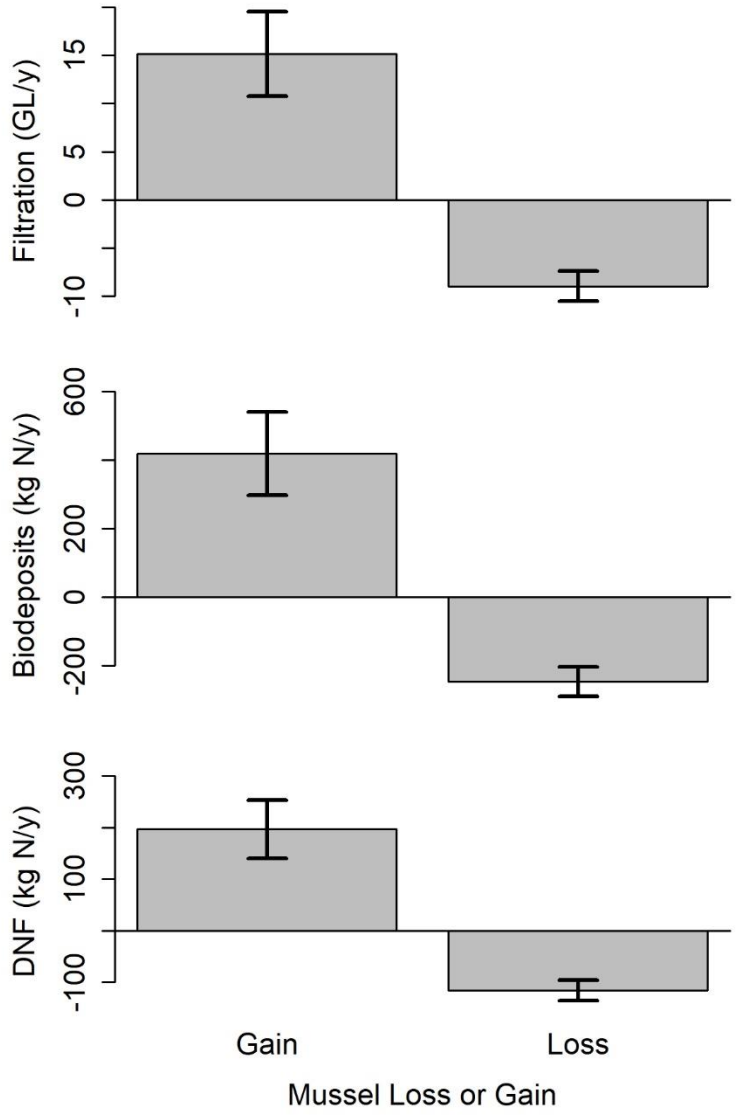

N
a
b
c
0 10 20 40 60 80
Kilometers
0.05
71.73
Mussel Abundance (millions)
–
0
+
Absolute Mussel Change

Figure 6


Filtration (GL/y)
-10
0
5
15
Biodeposits (kg N/y)
-200
0
200
600
DNF (kg N/y)
-100
100
300
Gain
Loss
Mussel Loss or Gain

VITA

Robert Isdell was born in Nassawaddox, Virginia on February 4, 1989. He grew up on the Eastern Shore of Virginia, where he lived until college. Robert graduated *summa cum laude* from the University of North Carolina at Greensboro with a B.S. in Biology in 2010. After college, Robert enrolled in the master's degree program at the College of William & Mary under Drs. Matthias Leu and Randolph (Randy) Chambers. He graduated in 2014 with a M.S. in Biology, and immediately began his Ph.D. at VIMS under the direction of Drs. Donna Bilkovic and Carlton (Carl) Hershner. Robert will graduate in 2018 with a Ph.D. in Marine Science.